

PLEISTOCENE MAMMALS FROM
THE LIMESTONE FISSURES
OF SZECHWAN, CHINA

EDWIN HARRIS COLBERT AND
DIRK ALBERT HOOIJER

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ERRATUM

The legend to figure 4 of plate 3 should read: Three tons of "dragon bones," the property of a whole-sale drug merchant.

CONTENTS

INTRODUCTION	7
Historical Background	8
Occurrence of the Yenchingkou Fauna	9
Relationships of the Yenchingkou Fauna to Recent Faunas of China	11
Relationships of the Yenchingkou Fauna to Other Extinct Cave Faunas of East Asia	15
Age of the Yenchingkou Fauna	18
Nature of the Material Comprising the Yenchingkou Fauna	20
Species and Subspecies in Fossil Materials	21
Acknowledgments and Abbreviations	25
SYSTEMATIC DISCUSSION OF THE YENCHINGKOU FAUNA	26
Primates	26
Cercopithecidae	26
<i>Rhinopithecus roxellanae tingianus</i>	26
Hylobatidae	27
<i>Hylobates (Bunopithecus) sericus</i>	27
Lagomorpha	29
Leporidae	29
<i>Lepus</i> sp.	30
Rodentia	30
Rhizomyidae	30
<i>Rhizomys sinensis troglodytes</i>	30
Hystricidae	40
<i>Hystrix</i> cf. <i>subcristata</i>	41
Carnivora	41
Canidae	41
<i>Cuon javanicus antiquus</i>	41
Ursidae	43
<i>Euarctos kokeni</i>	43
Procyonidae	46
<i>Ailuropoda melanoleuca fovealis</i>	46
Mustelidae	50
<i>Charronia flavigula tyrannus</i>	50
<i>Arctonyx collaris rostratus</i>	53
<i>Arctonyx collaris collaris</i>	55
Viverridae	56
<i>Viverra zibetha expectata</i>	56
Hyaenidae	60
<i>Crocota crocota sinensis</i>	60
Felidae	67
<i>Felis tigris</i>	67
<i>Felis</i> sp.	71
Proboscidea	71
Stegodontidae	71
<i>Stegodon orientalis</i>	71
Elephantidae	81
<i>Palaeoloxodon namadicus</i>	81
Perissodactyla	81
Chalicotheriidae	81
<i>Nestoritherium sinense</i>	81
Tapiridae	82

<i>Megatapirus augustus</i>	82
Rhinocerotidae	90
<i>Rhinoceros sinensis</i>	90
Artiodactyla	102
Suidae	102
<i>Sus scrofa</i>	102
Cervidae	105
<i>Rusa unicolor</i>	105
<i>Moschus moschiferus plicodon</i>	108
<i>Muntiacus muntjak margae</i>	110
<i>Elaphodus cephalophus megalodon</i>	113
Bovidae	116
<i>Bubalus bubalis</i>	116
<i>Bibos gaurus grangeri</i>	122
<i>Capricornis sumatraensis kanjereus</i>	127
<i>Naemorhedus goral</i>	129
BIBLIOGRAPHY	130

INTRODUCTION

IN THE EARLY AUTUMN of 1921 Dr. Walter Granger, paleontologist of the Central Asiatic Expeditions of the American Museum of Natural History, made a journey into the province of Szechwan, China, to investigate the possibilities of collecting fossil mammals in that region. This trip was made at the suggestion of the Director and certain members of the Geological Survey of China, who had obtained information from Mr. J. Langford Smith, at that time British Consul at Ichang on the Yangtze River, as to the presence of fossil bones in the vicinity of Wanh sien on the upper Yangtze. The trip, when undertaken, was for the most part a "shot in the dark," since the information on the nature and location of the fossils was indeed meager. Fortunately the expedition proved to be a huge success, so much so that Granger stayed at Yen ching kou, the fossil locality, through the winter and spring of 1921-1922, and returned for two additional seasons of collecting in the winters of 1922-1923 and 1925-1926. A large collection of choice fossil mammals of Pleistocene age was brought out and shipped to the American Museum of Natural History, and for the first time definite information as to the age and locality of these fossils, which previously had been described in part by various authors on the basis of very fragmentary remains, was obtained. An account of the collecting trips in Szechwan can be found in Granger (1932).

The fossils from Szechwan came from limestone fissures or pits at the tops of high Palaeozoic ridges which parallel the Yangtze River. These pits have been worked for many years by Chinese farmers, who sell the bones they obtain to druggists in the belief that they are dragon bones and are therefore efficacious in the treatment of many human ills. It was through the channels of Chinese drug stores and traders that most of the earlier fossils came to the attention of trained paleontologists—notably Owen, Koken, Schlosser, and Matsumoto. Granger was the first paleontologist to succeed in reaching the source of supply for these fossils and to supervise personally their collection.

The results of the work at Yen ching kou have been summarized by Granger in the fol-

lowing words: "The collections of the three years give a very adequate representation of the animal life of early Pleistocene times in this region. It is a fauna of which previously we had just an inkling through the descriptions of fragmentary specimens by Owen, Koken, and Matsumoto, of specimens probably obtained from drug merchants and others along the upper Yangtze and the exact source of which was not known. The collection is important not only as giving a picture of the life of this particular region but, being midway between fossiliferous deposits of the same age in north China and northern India, it helps greatly in working out the general distribution and migrations of mammalian life in eastern Asia during the Pleistocene period" (Granger, 1932, p. 528).

Within the past two decades extensive collections and studies have been made in the Pleistocene of Asia, particularly in India, Burma, Java, Indo-China, and at various localities in South and North China. As the result of this work our knowledge of the Quaternary succession of faunas in eastern Asia and the Orient has been growing and taking shape, and consequently it has become increasingly apparent that the many discoveries in the various regions and localities can be integrated to form a unified and logical interpretation of the Pleistocene mammals of Asia and of the environment in which they lived. The mammalian faunas of southern China are especially important in the study of the Asiatic Pleistocene, because they are intermediate, geographically, between the famous Choukoutien fauna of North China and the Trinil fauna of Java, both of which are associated with remains of early man. Of the South Chinese faunas, none is so rich either in the number of forms represented or in material belonging to each species as the assemblage collected by Granger at Yen ching kou.

Because of the importance of this large collection and the additional knowledge regarding Asiatic Pleistocene faunas that has been obtained since the preliminary report by Matthew and Granger, it has been thought advisable to make a thorough study of the fossil mammals from Yen ching kou.

The results of this investigation are set down in the following pages. In doing this work the present authors are merely following the intentions of Matthew and Granger, which because of a varied set of circumstances were never carried to an actual realization.

HISTORICAL BACKGROUND

The first Chinese fossils known to be from Szechwan were described by Owen in 1870 and consisted of a series of teeth obtained by Mr. Robert Swinhoe, a British diplomatic official in the Orient. These were said to be "from a cave, near the city of Chung-king-foo, in the province of Sze-chuen" (Owen, 1870, p. 421). From the fossils thus obtained, Owen described several new forms: *Stegodon orientalis*, *Hyaena sinensis*, *Rhinoceros sinensis*, *Tapirus sinensis*, and *Chalicotherium sinense*.

Fossils from Szechwan were next described and discussed by Koken in 1885 and by Schlosser in 1903. Their work has been briefly summarized by Matthew and Granger as follows: "Koken in 1885 described a collection secured by von Richthofen, apparently from the trading junks of the Yang-tse-kiang and understood by him to have come from far up the river in 'caves in Yun-nan.' Whether this was the real locality remains to be verified; one has the impression from the reading of von Richthofen's letter, quoted by Koken, that the traveller himself suspected that the locality might not have been correctly stated. It is certain at all events that the major part of Koken's collections, like Owen's, represent substantially the same faunal facies, and they seem to agree as to species, in part at least, with our collections. Koken also distinguishes an older fauna of supposed Lower Pliocene age, including *Hipparion*, *Camelopardalis*, *Palaeomeryx*, etc., which is more extensively represented in Schlosser's later collections, and is probably substantially the same fauna as the fine collections secured recently by J. G. Andersson and now being studied by Professor Wiman.

"Schlosser in 1903 described a large collection secured by Dr. Haberer for the Munich museum, and revised the work of Owen, Koken and other previous writers. He concluded that Owen's fauna, except

Stegodon, and most of Koken's material, was of Pleistocene age. There is no doubt, however, that the *Stegodon* is coeval with the rest of the fauna in Granger's collection, and one may assume that it was probably so in the Owen and Koken collections. Schlosser's material belonged mostly to the older Pliocene fauna distinguished by Koken and came from localities farther to the north" (Matthew and Granger, 1923, p. 565).

Subsequently, in 1915, Matsumoto brought out a very carefully prepared paper, containing numerous fine plates, describing a collection of fossil mammals obtained by Mr. T. Sakawa "in a certain marly district of Sze-chuan, China." Matsumoto recognized two faunas in the material before him, according to the manner in which the fossils were preserved. The first, which he designated as the "*Stegodon* fauna" was found in a "brown clay, which is evidently a decomposed product of lime-stone." These fossils were supposed by Matsumoto to be of Upper Pliocene age. The other fauna, which according to this author was found in a cave loam, he regarded as of Lower Pleistocene affinities.

Such was our knowledge of the fossil mammals from Szechwan at the time Granger made his first trip to Yenchingkou. Fragmentary fossils had been described by various authors, who had secured their materials largely through the channels of the Chinese drug merchants. It was only after the American Museum collections had been gathered together that a truly definitive knowledge of the Szechwan fossil mammalian fauna could be obtained. In 1923 Matthew and Granger published a brief description of the American Museum collection, and this represents a great advance over any previously existing knowledge regarding the Szechwan fossil mammals. This paper was frankly of a preliminary nature and therefore presented an incomplete picture of the Yenchingkou fauna.

Since the publication of Matthew and Granger's paper of 1923, and up until the writing of the present contribution, a few additional papers have been published bearing upon this problem in a specific way.

In 1929 (pp. 16-17) Osborn described as a new subspecies the *Stegodon orientalis* material from Yenchingkou, collected by Granger.

er. In 1934 (pp. 384–385) Colbert described a chalicotheres tooth from the Yenchingkou collection in connection with a broad study of chalicotheres from China and Mongolia. Young in 1935 (1935a) described a mammalian microfauna from this locality, listing 10 species or examples of bats, insectivores, and rodents hitherto unknown as members of the Yenchingkou fauna. This author admits, however, that his material was not collected *in situ* and that a majority of the forms recorded may very possibly be of post-Pleistocene age. A year later, Young described discoveries of fossil *Bubalus* in China and mentioned specimens from Yenchingkou. He pointed out (1936, p. 511) the fact that *Bubalus* remains already had been collected at this locality by Granger but had not as yet been described. In 1939 Young described new materials from the Yenchingkou sites collected by L. P. Chia. These fossils, though for the most part fragmentary, supplement and add to the materials described by Matthew and Granger.

In the meantime Granger (1938) published a semi-popular account of his discovery of a complete gaur skeleton at the Yenchingkou pits and included a photograph of the specimen as it is now mounted at the American Museum of Natural History.

Finally, Hooijer has recently published two papers (1947a, 1951a) describing some tigers and two new deer in the American Museum collection from Yenchingkou.

As a result of these several papers, together with the contributions made in the present work, the fossil fauna from Yenchingkou is constituted as follows:

Primates

Cercopithecidae

Rhinopithecus roxellanae tingianus Matthew and Granger

Hylobatidae

Hylobates (Bunopithecus) sericus Matthew and Granger

Lagomorpha

Leporidae

Lepus sp.

Rodentia

Rhizomyidae

Rhizomys sinensis troglodytes Matthew and Granger

Hystriidae

Hystrix cf. *subcristata* Swinhoe

Carnivora

Canidae

Cuon javanicus antiquus Matthew and Granger

Ursidae

Euarctos kokeni (Matthew and Granger)

Procyonidae

Ailuropoda melanoleuca fovealis Matthew and Granger

Mustelidae

Charronia flavigula tyrannus, new subspecies

Arctonyx collaris rostratus Matthew and Granger

Arctonyx collaris collaris Cuvier

Viverridae

Viverra zibetha expectata, new subspecies

Hyaenidae

Crocuta crocuta sinensis (Owen)

Felidae

Felis tigris Linnaeus

Felis sp.

Proboscidea

Stegodontidae

Stegodon orientalis Owen

Elephantidae

Palaeoloxodon namadicus (Falconer and Cautley)

Perissodactyla

Chalicotheriidae

Nestoritherium sinense (Owen)

Tapiridae

Megatapirus augustus Matthew and Granger

Rhinocerotidae

Rhinoceros sinensis Owen

Artiodactyla

Suidae

Sus scrofa Linnaeus

Cervidae

Rusa unicolor (Kerr)

Moschus moschiferus plicodon, new subspecies

Muntiacus muntjak margae Hooijer

Elaphodus cephalophus megalodon Hooijer

Bovidae

Bubalus bubalis (Linnaeus)

Bibos gaurus grangeri, new subspecies

Capricornis sumatraensis kanjereus, new subspecies

Naemohedus goral (Hardwicke)

OCCURRENCE OF THE YENCHINGKOU FAUNA

The little hamlet of Yenchingkou is about 10 miles up the Yangtze River from the city of Wanhhsien and about 10 miles inland from the south bank of the river. Granger has described its situation as follows: "Arriving at Yen-ching-kou, I found the village nestled at

the base of a great ridge of Palaeozoic limestone which had been thrust up in remote times through the Permo-Mesozoic red beds. The ridge rose abruptly nearly 2,000 feet above the valley and was nearly fifty miles long. It was the conspicuous feature of the landscape as one looked south from the Yangtze River which parallels the ridge ten miles away" (Granger, 1932, p. 513).

The Yenchingkou fossils came from the top of this ridge and their mode of occurrence is thus described by Granger: "Limestone is mildly soluble in rain water, especially water which has soaked through humus and decaying vegetation. Such water gathering in pools on top of the limestone ridge had in times past, when the region was forested, dissolved out shafts in the rock—sometimes to a depth of one hundred feet—often to fifty feet or more. The soluble parts of rock passed on down through cracks and the residue remained as mud in the bottom of the pit. These shafts were really vertical caves, and the action which produced them was similar to that which produces horizontal caves.

"The majority of the shafts or pits seem to have been of Pliocene or early Pleistocene origin, and they are for the most part filled to-day with yellowish or reddish mud which had flowed in from the surface or had been left as undissolved residue. There were times, however, when they were open and evidently acted as pitfalls for the various animals which inhabited the region. At any rate the fossil bones were being found in the mud filling of the pits—and usually at depths of twenty feet or more. It was quite evident that the bones got into the pits in two ways. When a complete skeleton was found in a pit it seemed almost certain that the animal had fallen in and either had been killed by the fall or had died of starvation. On the other hand, when single elephant teeth, sometimes considerably weathered, were found, it seemed obvious that the animal had died on the surface, its skeleton had become disorganized and parts of it had gradually drifted into the pit by gravitation.

"A few such pits as these are being formed to-day along the top of the ridge, and undoubtedly they still occasionally act as traps for unwary animals that stray too close to the edge, which is usually masked by a dense

undergrowth. Some of these open pits have diameters of fifty feet or more—real sink-holes—but more often they are smaller—eight or ten feet across. The pits as observed are rather unevenly distributed along the fifty miles of ridge top, although this may be simply because certain areas are more denuded than others and the pits consequently are more easily located" (p. 514).

It is from these pits that bones are procured for the Chinese drug trade. Most of the prospecting and digging of the pits is done by Chinese farmers in the fall and winter, after the summer crops are harvested and the winter crops are planted. The bones thus discovered are then sold to drug merchants by weight. In the digging out of the bones, crude mining methods are followed. One or two men may be lowered into the pit by means of a rope rigged on a pulley supported by poles directly over the center of the pit. The mud and residue in the bottom of the pit are dug out and shoveled into wicker baskets, which are raised to the surface by the winch. This deposit is searched for bones, and such bones as are found are scraped clean and piled up in some convenient farmhouse to dry.

Granger found that the most practicable way to procure fossils from the pits was to make frequent visits along the top of the limestone ridge and to purchase from the native diggers the best of the fossils procured by them. By spending three winters in the vicinity of Yenchingkou, by careful purchasing of the fossils on the spot, so that the exact pit for each specimen was known, and by paying bonuses to the diggers for unusually complete specimens, he obtained a collection of Pleistocene mammals that at the present time is quite unsurpassed.

Matsumoto considered the Szechwan fossils as belonging to two distinct faunas, an older or "*Stegodon* fauna" regarded as of upper Pliocene age, and a younger fauna from the "cave-loam" placed by him in the lower Pleistocene. The work of Granger at Yenchingkou does not bear out Matsumoto's supposition of two faunas of distinct and different ages. What Granger did determine, however, was the fact that there was an "ecologic stratification" of the Yenchingkou fauna, based on the altitude of the pits on

the top of the limestone ridge and on the assumption that the topography of the top of the ridge has not changed greatly since early Pleistocene times.

"It was interesting to note that the pits in the lower areas contained animals not frequently found in pits high up on the knolls. *Stegodon*, *Rhinoceros*, the giant tapir and the gaur were, as might be expected, confined pretty much to the lower pits, while the deer and goats were found more abundantly in the pits higher up. One would naturally expect large animals to keep more or less to the lower levels, while the deer and goats would frequent the hills" (Granger, 1932, p. 517).

RELATIONSHIPS OF THE YENCHINGKOU FAUNA TO RECENT FAUNAS OF CHINA

A list is given above of all the genera and species of mammals now known to be included in the extinct fauna from the fissure fills at Yenchingkou. In a general way this extinct fauna is compared here with the recent faunas of China, to see what resemblances and differences exist between the fossil and the recent assemblages, and to interpret, if possible, the significance of the comparisons.

It is obvious that the Yenchingkou fauna should resemble certain of the recent faunas of China more than others, since China and Mongolia cover a vast area in which are included several zoogeographic divisions of greater or lesser extent, and it is to be expected that the Yenchingkou fauna would be most closely related to the modern fauna living in a habitat most closely resembling that in which the Middle Pleistocene mammals of Szechwan lived.

Glover Allen in his monograph on the mammals of China and Mongolia (1938) lists seven faunal areas, some of which are in the great Palearctic zoogeographic realm while others are in the Oriental realm, as follows:

1. The Northern Forest, roughly north of the northern boundary of Mongolia, extending through Manchuria and into the northern part of Hopei Province east of the Khingan Range.
2. The Gobi, including Inner and Outer Mongolia and Sinkiang.
3. North China, composed of southern Hopei

Province, Shantung, Shansi, Shensi, Kansu, and the northern portion of Honan, bounded on the north by the Gobi and on the south by the Min Shan and Tsingling ranges.

4. South China, generally speaking the lowland area south of the thirty-fourth parallel and east of the Western Highlands; containing Kiangsu, Anhwei, Hupeh, Hunan, Kiangsi, Chekiang, and Fukien Provinces.

5. The Western Highlands, principally of Szechwan but including parts of Kweichow and Yunnan.

6. The Subtropical region, a northeastern extension through southern Yunnan, Kwangsi, and Kwangtung of conditions typical of Burma and Indo-China.

7. The Tibetan Plateau, the high land west of Szechwan and north of the Himalayas.

An examination of table 1 will show that numerically the extinct fauna of Yenchingkou is most closely related to the recent fauna of the Western Highlands of Szechwan. This is about as would be expected, since, as Granger pointed out, there is every reason to think that the topography of Szechwan was not much different in Pleistocene times than it is at present. Moreover, the climate, while not exactly the same, was similar enough to the present climate so that there is a strong resemblance between the fauna living in the region at that time and the present fauna in the same area. In addition to the general broad similarities thus indicated between the extinct and recent faunas of the Szechwan highlands, more definite relationships between the assemblages can be classified as follows:

1. Many mammals in the Yenchingkou fauna are very similar to their modern counterparts living in the same region or in nearby parts of China. These animals constitute the bulk of the fauna, and their general prevalence gives to the Yenchingkou assemblage its "modern look."

2. But a certain proportion of the Yenchingkou fauna consists of animals that no longer are found in this portion of Szechwan but that persist in modern times in more distant portions of China or of Asia, or in a few cases in other parts of the world.

3. Finally, a portion of the Yenchingkou fauna is made up of completely extinct genera and species. It is these animals that give to the fauna its "ancient look," and it

TABLE 1
COMPARISON OF THE YENCHINGKOU FAUNA WITH MODERN ASIATIC FAUNAS

	1. North- ern Forest	2. Gobi	3. North China	4. South China	5. West- ern High- lands	6. Sub- tropical	7. Tibet	Yenching- kou
<i>Rhinopithecus</i>					x			x
<i>Hylobates</i> " <i>Bunopithecus</i> "						x		x
<i>Lepus</i>		x	x	x	x		x	x
<i>Rhizomys</i>				x	x	x		x
<i>Hystrix</i>				x	x	x		x
<i>Cuon</i>	x	x	x	x	x	x		x
<i>Euarctos</i>			x	x	x	x		x
<i>Ailuropoda</i>					x			x
<i>Charronia</i>	x		x	x	x	x		x
<i>Arctonyx</i>	x		x	x	x	x		x
<i>Viverra</i>				x	x	x		x
<i>Crocuta</i>								x
<i>Felis</i>	x	x	x	x	x	x		x
<i>Stegodon</i>								x
<i>Palaeoloxodon</i>								x
<i>Nestoritherium</i>								x
<i>Megatapirus</i>								x
<i>Rhinoceros</i>								x
<i>Sus</i>	x		x	x	x	x		x
<i>Rusa</i>					x	x		x
<i>Moschus</i>	x		x	x	x			x
<i>Muntiacus</i>				x	x	x		x
<i>Elaphodus</i>				x	x			x
<i>Bubalus</i>								x
<i>Bibos</i>								x
<i>Naemorhedus</i>			x	x	x			x
<i>Capricornis</i>				x	x	x		x
Total number of genera	6	3	9	15	18	13	1	27

is the extinction of these forms that causes, for the most part, the real differences of the Yenchingkou mammalian assemblage from the modern mammalian fauna of western China.

What are the significant facts to be found in the extinction of certain members of the Yenchingkou fauna, and in the relationships that are shown between other elements in the assemblage and their modern counterparts? These are questions that deserve a certain amount of attention.

As mentioned above under 3, the outstanding difference between the Yenchingkou mammalian assemblage and the modern fauna from this part of China is the complete extinction of certain genera [(*Bunopithecus*), *Stegodon*, *Palaeoloxodon*, *Nestoritherium*, and

Megatapirus] during the transition from middle Pleistocene to Recent times.

Except for *Bunopithecus* (a subgenus of doubtful validity), these are large mammals and for that reason are particularly conspicuous in the Yenchingkou fauna. Since none has exact counterparts living at the present time it is difficult to attempt an interpretation of their extinction. Suffice it to say that they seem to have been the victims of a general world-wide trend marking the transition from Pleistocene to Recent times whereby certain large mammals ranging widely over the several continents were caught in a "wave of extinction" during the final phases of the glacial period.

Those forms that no longer are to be found in the western Szechwan highlands but that

still persist in other parts of the world (*Crocota*, *Rhinoceros*, *Bibos*, and *Bubalus*) combined with the extinct types contribute to the Yenchingkou fauna most of the differences distinguishing it from the recent fauna of western China. Of these forms all but the hyena (*Crocota*) are found in portions of Asia adjacent to or near Szechwan. *Crocota* is at the present time limited to the Ethiopian region.

This brings us to a consideration of the bulk of the Yenchingkou fauna, which consists of animals not so greatly different from their modern counterparts living in Szechwan. Generally speaking, it can be said that the Pleistocene mammals of Szechwan are very similar to the corresponding modern types in this region, except that in most cases the extinct animals are larger than their modern relatives.

This distinction occurs time and again in the comparisons between Pleistocene and prehistoric mammals and modern types. One of us (Hooijer, 1949, 1950) has cited several examples from the East Indies islands, and the phenomenon is apparently world-wide. Naturally, the supposition is that this decrease in general size during the Quaternary is correlated with the warming-up of the world's climates since the Ice Age (see Romer, 1949, pp. 111-112; and Simpson, 1949, p. 136). However, there are some exceptions to this "rule" (Hooijer, 1950, pp. 147-148), which seems to indicate that the general decrease in size in the course of time is not controlled by environmental factors exclusively.

In the case of the Yenchingkou mammals, it seems that most fossil mammals are the direct ancestors of the modern related types in this region of Asia. Thus we must assume that there has been a general decrease in size from Pleistocene ancestor to Recent descendant in this area as well as elsewhere. This change may have been brought about, as stated already several years ago by one of us (Colbert, 1949, p. 129), by the gradual transition from a generally cool climate in western China in middle Pleistocene times to a rather warm climate at the present time. Thus there may have been a working of Bergmann's principle through time: as the climate became increasingly warmer during

the passage from the middle Pleistocene to the Recent the succeeding generations of mammals became successively smaller.

In the present case, however, it seems that there may be still another explanation for the differences between the Szechwan fossil mammals and their recent counterparts. The province of Szechwan is at present a very hilly or mountainous region, and it is probable (as suggested above) that much the same geographic conditions as are now developed were characteristic of the region in middle and late Pleistocene times. If so, there is reason to believe that with the generally cooler temperatures supposedly prevailing in those days there was a certain disparity in temperatures between the lowlands and the uplands. Consequently, it is possible that the fossil fauna from the Szechwan pits, coming as it does from the tops of the peaks and ridges, was in reality a "cool-climate fauna" ecologically limited to the highlands, while there was a correlative fauna (not represented by fossil remains) of corresponding but smaller types living in the lowlands. Then with the general increase in the average temperature consequent upon the transition from the Pleistocene to Recent times, the upland fauna of large types may gradually have become extinct, to be succeeded by the lowland fauna or smaller types invading the upland regions as they followed the ascent of the isotherms up the mountainsides. This argument can be applied to many of the elements in the Yenchingkou fauna—elements that are found represented in this same region today by corresponding but smaller animals.

Yet there are certain members of the Yenchingkou fauna to which this explanation does not readily apply, since they are not represented at the present time by corresponding types in this portion of Szechwan. Therefore, as an alternative explanation, it is reasonable to suppose that some of the Yenchingkou Pleistocene mammals may have been forced out of this region as the climate became warmer, to seek elsewhere a refuge in cooler areas at higher altitudes. Such an emigration would be to the west, and it is in the extreme western portion of Szechwan, characterized by rugged topography running up to considerable heights, that the giant

panda, *Ailuropoda*, and the golden monkey, *Rhinopithecus*, animals formerly living at Yenchingkou, are now found.

None of the above explanations need apply exclusively to the entire fossil fauna of Szechwan. Indeed it is very likely that there was a combination of circumstances that led to the size differences that distinguish the modern Chinese fauna from its Pleistocene antecedent. There may have been a combination of regressive size growth, plus extinction and replacement, plus emigration. The purpose here is not to attempt any definite explanation for the phenomena observed but to suggest the possibilities that might variously explain them.

Other considerations besides those of size differences can be presented with regard to this comparison of the fossil and recent faunas of Szechwan in their relationships to past and present climates. For instance, some of the genera of mammals living in Szechwan during the Pleistocene which since have become entirely extinct, such as *Stegodon* and *Nestoritherium*, have no close modern relatives, so that speculation regarding them is of little avail. Others, however, particularly the genus *Megatapirus*, have closely related genera living at the present time outside China. *Megatapirus* lived in Szechwan; its modern relative, *Tapirus*, inhabits the Malay Peninsula and Sumatra. Why did not *Tapirus* succeed *Megatapirus* in Szechwan? In this case, it seems very probable that although there was a rising temperature accompanying the change from Pleistocene to Recent conditions in western China, the rise was not sufficient to permit certain tropical forms such as the modern tapir to replace its cool-climate predecessor. Of course this may not be the only factor involved in the case of the tapirs. The disadvantages of rough topography might also have been effectual in preventing the modern *Tapirus* from invading Szechwan subsequent to or during the extinction of *Megatapirus*. But it seems likely that climate was a more potent barrier in this case than were topographical conditions.

Certain elements in the fossil fauna of Szechwan are hard to explain on the basis of our knowledge of recent related animals. Such is the case of the gibbon (*Hylobates* or *Bunopithecus*) at Yenchingkou, the hyena (*Crocuta*), the rhinoceros (*Rhinoceros*), and

the gaur (*Bibos*). At present these animals live in regions outside China and in habitats that are essentially hot or tropical. Why should such animals have lived in Szechwan in Pleistocene time when climatic conditions, so we think, were much cooler than they are now? If these animals were capable of living in the cool climate of the Pleistocene in Szechwan, why did they become completely extinct in this habitat, even though their closely related modern counterparts persist in distant, tropical regions? This case is somewhat different from that of the tapirs, discussed above. In the case of the tapirs, we are dealing with different genera, sufficiently distinct to presuppose ecological adjustments of such magnitude as to account for the one living in a cool climate and the other in a tropical region. But in the cases of the gibbon, the hyena, the rhinoceros, and the gaur, the fossils are so nearly like their modern representatives that it is difficult to understand why the fossil forms should have been supposedly cool-climate types and the modern ones warm-climate types. Or, rather, it is difficult to understand why, if these animals were able to live in Szechwan during the Pleistocene, they were unable to persist into a period of warmer temperatures when very closely related modern types are able to withstand tropical conditions.

Then the elements in the fossil fauna of Szechwan to which none of the above speculations need apply are the forms that are so nearly like the modern related types in size that it is not necessary to account for their presence in past and present faunas as the result of changing ecological conditions. In other words, some of the Yenchingkou mammals must have been directly ancestral to their modern counterparts in this region, surviving the climatic changes that took place with the passage of time without showing corresponding physical changes. In this category may be placed the civet (*Viverra*) of Yenchingkou, which shows certain minor qualitative differences but no essential quantitative differences from the modern *Viverra* in the same region.

Finally, there is the question of why certain elements which might logically be expected are absent from the Yenchingkou fossil fauna. In some cases these absences are undoubtedly due to the accidents of preser-

vation and collecting. Such an explanation is readily applicable to the small insectivores, of which a considerable number exist in the present fauna of Szechwan but which are virtually unrepresented in the fossil fauna. Because of their small size it is likely that the bones of these animals did not withstand the rather rigorous conditions of burial typical of the Yenchingkou sediments. The same is probably true with regard to the bats and to a lesser extent the rodents and hares. In this connection it is interesting to note that such rodents as are found in the Yenchingkou fauna are forms of rather large size, such as *Rhizomys* and *Hystrix*. Even with these two forms the implications are peculiar. Why should *Hystrix*, a very prominent member of Pleistocene faunas in other parts of eastern Asia, be so sparsely represented at Yenchingkou? Why should *Rhizomys* be so unusually abundant in this particular fossil fauna?

It may be that another factor of importance in an explanation of the lack of small mammals (except *Rhizomys*) in the Yenchingkou fauna is the relationship of climbing ability to body size and gravity. The occurrence of a great proportion of the fossil remains at Yenchingkou is probably due to animals' having inadvertently fallen into the pits when these pits were open and deep. Thus many large forms were trapped and killed. But small mammals like insectivores and rodents would in the first place be but slightly injured by falling into these pits, and in the second place would in many cases be able to climb out because of their ability to cling to the rough surface of the sides of the pits with sufficient effectiveness to overcome the downward pull of gravity. Moreover, it is likely that these small mammals would not blunder into the open pits as would large animals. The small forms would become aware of the danger in time to avoid it, and would be able to cling to vegetation growing around the pits and in this manner escape falling in.

Again it is probable that the methods of collecting have had a considerable effect on the composition of the microfauna from the Yenchingkou pits. All the collecting to date has been done by natives, searching for "dragon bones." It is therefore quite probable that careful sieving would bring to light

from the Yenchingkou pits a microfauna that is still but little known.

However, these considerations do not apply to the larger forms that are present in the recent fauna of the Szechwan region but that are unknown from Yenchingkou. These are specifically certain carnivores and a few artiodactyls: *Ailurus*, *Ursus*, *Nyctereutes*, *Vulpes*, *Mustela*, *Lutra*, *Micraonyx*, *Viverri-cula*, *Paguma*, *Cervus*, and *Budorcas*.

The absence of some of these genera from the Yenchingkou fauna may be explained in several ways. The region of Yenchingkou and Wanhhsien may have been too far east for *Ailurus* and *Ursus* during Pleistocene times, as today it is too far north for *Micraonyx*, and too far east or south for *Cervus*. Even so it is difficult to see why, if *Ailuropoda* and *Rhinopithecus* (now found to the west of Yenchingkou) could live in eastern Szechwan in Pleistocene times, the same should not apply to *Ailurus*. The same argument can be applied to some of the other forms here considered. The absence of *Lutra* from the Yenchingkou fauna may be explained by the aquatic habits of this animal, which would preclude its inclusion in an upland fauna.

But as for the other genera listed, their absence from the Yenchingkou fauna is indeed difficult to understand, especially since most of them are animals of considerable size, living at the present time in the vicinity of Wanhhsien. The solution to this question must await further studies at a future date.

The absence from the Yenchingkou fauna of other genera now found in regions distant from the Western Highlands of China and not found in these highlands is so obvious as to need no comment. As is shown below, this geographic and regional separation explains many of the differences between the North Chinese fauna of Choukoutien and that of Yenchingkou, assemblages probably contemporaneous in time but quite different in habitat.

RELATIONSHIPS OF THE YENCHINGKOU FAUNA TO OTHER EXTINCT CAVE FAUNAS OF EAST ASIA

A number of cave faunas have been discovered in east Asia, principally in China and Indo-China, which compare very well with the characteristic fauna of Yenchingkou.

TABLE 2
GENERAL COMPARISON OF CAVE FAUNAS OF EAST ASIA

	Yenching-kou	Hoshang-tung ^a	Tan-yang ^b	Mogok	Kweilin ^c	Lang Son ^d	Tam Nang ^e
<i>Rhinopithecus</i>	x						
<i>Hylobates</i>							
" <i>Bunopithecus</i> "	x						
<i>Lepus</i>	x						
<i>Rhizomys</i>	x						x
<i>Hystrix</i>	x	x	x	x	x	x	x
<i>Cuon</i>	x						x
<i>Euarctos</i>	x	x	x		x	?	?
<i>Ailuropoda</i>	x	x		x	x		x
<i>Charronia</i>	x						
<i>Arctonyx</i>	x	x	x		x		x
<i>Viverra</i>	x				(x)		
<i>Crocuta</i>	x	x	x		x		x
<i>Felis</i>	x	x			x	x	x
<i>Siegodon</i>	x	x		x	x	x	x
<i>Palaeoloxodon</i>	x	x	x	x	(x)	x	x
<i>Nestoritherium</i>	x						
<i>Megatapirus</i>	x	x	x			x	x
<i>Rhinoceros</i>	x	x	x	x	x	x	x
<i>Sus</i>	x	x	x	x	x	x	x
<i>Rusa</i>	x	x	x	x	x	x	x
<i>Moschus</i>	x				(x)		
<i>Muntiacus</i>	x	x	x				x
<i>Elaphodus</i>	x						
<i>Bubalus</i>	x					x or	x
<i>Bibos</i>	x					x	x
<i>Naemorhedus</i>	x						x
<i>Capricornis</i>	x						

^a Present at Hoshangtung, but not at Yenchingkou: *Macaca*, *Pongo*, *Ailurus*.

^b Present at Tanyang, but not at Yenchingkou: *Macaca*, *Rattus*, *Paguma*, and *Hydropotes* (?).

^c Present at Kweilin, but not at Yenchingkou: *Macaca* and *Pongo*. In parentheses are recorded the genera not found *in situ* in the cave but bought in drug stores.

^d Present at Lang Son, but not at Yenchingkou: *Nesokia* (?).

^e Present at Tam Nang, but not at Yenchingkou: *Macaca*, *Pongo*, *Canis*, *Paradoxurus*, *Cervus*, *Proboscophilus*, and *Spirocerus*.

kou. These faunas are those of:

Hoshangtung cave, Yunnan (Young, 1932b; Bien and Chia, 1938)

Tanyang cave, Kiangsu (Pei, 1940)

Mogok caves, Upper Burma (Colbert, 1943)

Kweilin cave, Kwangsi (Pei, 1935)

Lang Son, Tonkin, Indo-China (Mansuy, 1916; Patte, 1928)

Tam Nang, Indo-China (Arambourg and Fromaget, 1938)

From table 2 it is apparent that the several Middle Pleistocene faunas of southeastern Asia are very much alike, in fact almost identical, which is about what would be expected

on the basis of a study of the modern mammalian faunas of China. Here we see the differences between two zoogeographic areas. The Yenchingkou, Tanyang, Kweilin, Hoshangtung, and Mogok faunas are situated in what is now the Oriental zoogeographic realm. To the north is the Choukoutien fauna, situated in what is at the present time the Palearctic zoogeographic realm. The southern faunas are quite different from the northern fauna; therefore there is good reason to think that some sort of zoogeographic division, similar to that existing at the present time, caused the extinct faunas of North

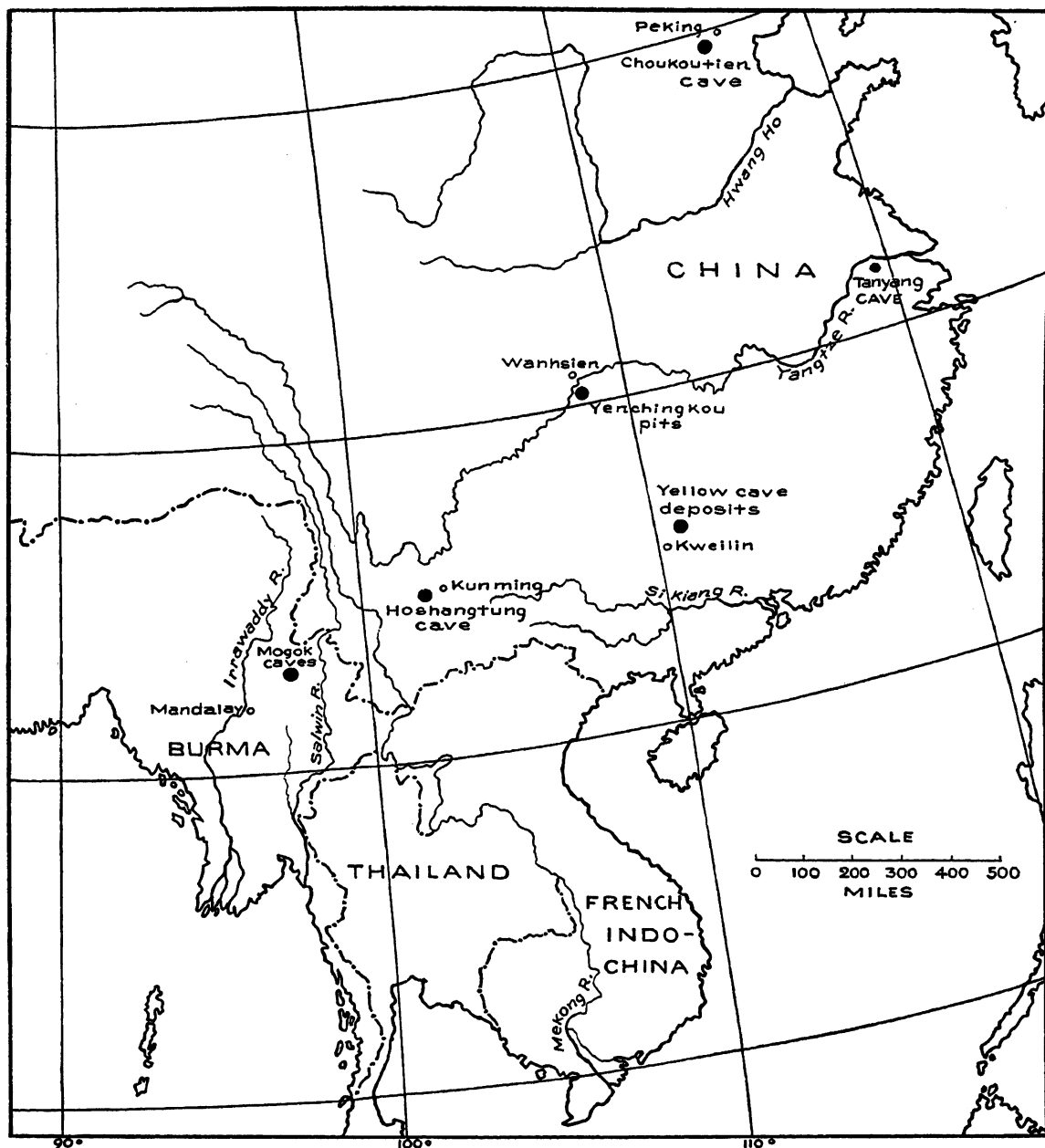


FIG. 1. Map of southeastern Asia showing Pleistocene fossil localities.

and South China to be distinct and different from each other, a fact that has been already pointed out by Teilhard, Pei, and others.

In discussing the characters of the fauna found in the Kwangsi caves, Pei wrote: "Most obviously the fauna found in Kwangsi associated with the Yellow cave-deposits

is the same as the Wanhsten fauna of Ssuchuan (see Matthew and Granger, 1923) and as the fauna of Yunnan recently described by Dr. C. C. Young from Yunnan.

"Thus it becomes clearer every day, that during the Lower Pleistocene times a single large faunistical unit of Indo-Malay-

sian affinities, characterized by *Stegodon*, *Tapir*, *Rhinoceros sinensis* (cf. *indicus*), *Hyaena ultima*, *Ailuropus* and (at least in the southernmost part of China) *Orang*, was largely spread over Southeastern China.

"Southward and westward, this faunistic block seems to fuse with the *Stegodon* fauna of Indo-China and Java, and to extend in the direction of India (*Orang* is known in the Siwalik deposits,¹ and *Ailuropus* has been described by Sir A. Smith Woodward from Burma).

"Northward, an abrupt change occurs at the latitude of the Tsinling range, north of which (for instance in Choukoutien) another, a widely different faunal assemblage, is found in the Lower Pleistocene, as characterized by the Euryceroid Deer, a special *Hyaena*, *Machairodus* and the *Dicerorhinus* types of *Rhinoceros* (*R. mercki* and *R. tichorhinus*).

"A few elements only of the southern block seem to have forced their way at that period, probably along the sea, up to the Huangho basin: the water Buffalo, *Hyaena ultima* (at the end of the period), and perhaps (unless he or his predecessor was already there) *Sinanthropus*" (Pei, 1935, p. 424).

It might be said here that the resemblances between the several southern faunas listed above go beyond generic relationships, so that there is a close specific identity between them. The conclusion following is that these faunas were contemporaneous, forming, as Pei has termed it, a "southern block" of Pleistocene mammals showing intergrading relationships much the same as are shown by modern mammals in this same general area.

AGE OF THE YENCHINGKOU FAUNA

In the original description of the fossils from Yenchingkou, Matthew and Granger designated them as of upper Pliocene age, a decision influenced largely by the presence of *Stegodon* and *Chalicotherium* (= *Nestoritherium*) in the fauna. At that time these two genera were considered as characteristic

Upper Tertiary types, a view based in large part on the older theories regarding the correlation of the Siwalik series in India.

During the past two decades or so, however, there has been a considerable shift of opinion regarding the age of the Siwaliks, especially the upper portion of the series, so that now the persistence of *Stegodon* and *Nestoritherium* into the Pleistocene is generally recognized. Consequently there have been new evaluations of the Upper Cenozoic faunas of China, and although differences of opinion exist there is general agreement that the Yenchingkou fauna and similar cave faunas from other parts of southern China are of Pleistocene age.

This being the case, how is the Yenchingkou fauna to be correlated within the Pleistocene? What are the relationships of this and contemporaneous faunas to other Pleistocene faunas of southeastern Asia, and in what portion of the Pleistocene period are these several faunas to be placed?

To begin this consideration, it should be mentioned that the position of the Yenchingkou fauna and other mammalian assemblages within the Pleistocene depends, to some extent, on one's definition of the limits of this geological period. Teilhard de Chardin (1937) regards the Villafranchian of Asia as of upper Pliocene age, basing his conclusions largely on diastrophic evidence, the rejuvenation of the topography and the cutting of the Fenho gorges in post-Villafranchian times being regarded by him as the logical break between the Pliocene and the Pleistocene. On the other hand, it is the inclination of the present writers to regard the world-wide spread of certain new mammalian types, particularly *Equus*, *Archidiskodon*, and *Bos* (in the broad sense of the term), as indicative of the advent of Pleistocene times. Therefore we would regard the Villafranchian in Europe and Asia as of lower Pleistocene age, since here are found these new mammalian types, which would place the diastrophic movements in China resulting in the cutting of the Fenho gorges within the Pleistocene.

It is obvious therefore that certain formations or faunas designated by Teilhard as of upper Pliocene age are here regarded as being included within the lower portions of the Pleistocene, while the beds and their con-

¹ The alleged occurrence of "*Simia* cf. *satyrus*" in the Upper Siwaliks of India has found its way into the literature, but, as already stated by one of us (Hooijer, 1948, p. 290, footnote), the evidence is inconclusive, and it would seem best for the present to remove *Pongo* from the faunal list of the Siwaliks.

tained faunas placed by Teilhard in the lower Pleistocene are here accorded a somewhat higher or later position.

As is shown above, there can be but little doubt that the various cave faunas in southeastern Asia showing the association of *Stegodon*, *Ailuropoda*, and *Hystrix* are contemporaneous with one another. Thus we may regard the faunas of Tanyang, the Kwangsi caves, Hoshangtung, Yenchingkou, and Mogok as separated elements of a single southeastern fauna that lived in Pleistocene times across southern China, Burma, and the Malay region. Moreover there is good reason to regard the southeastern Asiatic fissure deposits containing these faunas as about the equivalent of the Boulder Conglomerate complex in the Siwalik series of India. This last statement is based on the observations by Teilhard and de Terra in Burma, whereby it seems evident that the Mogok fissure deposits are probably correlative with adjacent boulder fans, these latter seemingly equal in age to the Boulder Conglomerate deposits of India. Extended arguments have been presented (Colbert, 1942a, p. 1447) supporting the assignment of the Boulder Conglomerate to a position well up within the Pleistocene, possibly in the Middle Pleistocene, and above the Pinjor and Tatrot beds in which are found faunas of essential Villafranchian aspects. Therefore the Mogok fauna, and by implication the other cave and fissure faunas contemporaneous with it, takes a position considerably above the bottom of the Pleistocene, and it seems not unreasonable to regard this position as coming at about the middle of the Pleistocene period, stratigraphically and temporally.

Antecedent to the Mogok fauna in Burma is the Upper Irrawaddy fauna, which by its aspect is clearly contemporaneous with the Pinjor fauna of India. Thus the relationship in India of a Lower Pleistocene deposit containing a Villafranchian fauna, the Pinjor, and succeeded by a later series, the Boulder Conglomerate, is repeated in Burma by the Lower Pleistocene Irrawaddy sediments containing the Upper Irrawaddy fauna of Villafranchian age, succeeded by the later, possibly Middle Pleistocene Mogok fissure deposits with their contained fauna (Colbert, 1943).

Similarly the same general relationships seem to hold in Yunnan, where the Ma Kai Valley deposits, containing a fauna that seems to be more or less comparable with the Irrawaddy-Villafranchian assemblage, apparently is succeeded by the Hoshangtung cave deposits, the fauna of which is so clearly contemporaneous with that of Mogok (Colbert, 1940). In Kwangsi and in Szechwan, respectively, there are at the present time no faunas known that would correspond with the Pinjor-Irrawaddy-Ma Kai complex, but, as is mentioned above, the faunas of Kweilin and related caverns in Kwangsi and of the Yenchingkou pits in Szechwan are clearly correlative with Mogok and Hoshangtung, while the fauna of the Tanyang cave deposits in Kiangsu shows this same relationship.

Finally we come to a consideration of the deposits and faunas in North China, specifically the Nihowan or Sanmen fauna, the fauna from locality 18, near Peking, admittedly of Villafranchian relationships and placed by Teilhard in the Upper Pliocene, and the Choukoutien fauna, assigned by this author and his associates to the Lower Pleistocene. The Nihowan fauna, in which *Equus* makes its first appearance in China, is certainly correlative with the other Villafranchian faunas mentioned above, namely, Pinjor, Upper Irrawaddy, and Ma Kai, and in the scheme considered here is to be regarded as of lower Pleistocene age. The Choukoutien fauna, coming later than the Nihowan assemblage, would therefore be reasonably expected as about the equivalent in age of the cave faunas in southern China and Burma, even though because of zoogeographic differences its elements do not correspond closely to those of the southern cave faunas. Consequently, in the present correlation Choukoutien may be considered as well up in the Pleistocene, perhaps about middle Pleistocene in age.

The only other alternative in the present scheme of correlation would be to place all the southern cave faunas and the Choukoutien fauna to the north, seemingly correlative with them, in the upper portion of the Lower Pleistocene. This is a possibility to be considered, and may be adopted if the reader prefers to accord to these faunas this earlier relationship. The only arguments to

be brought against such a procedure are that it assigns to the lower Pleistocene deposits of India a very considerable thickness, while among the cave faunas of China it assigns to the Lower Pleistocene many types which by their relationships and preservation seem to be later than might be expected of early Pleistocene fossils. Thus among the mammals constituting the Yenchingkou fauna are many forms only subspecifically separable from their modern counterparts, and this in some cases on very small degrees of difference. Moreover the fossilization of these Yenchingkou types is not so great as might be expected in early Pleistocene fossils, although it is of appreciable extent. This is exclusive of the Yenchingkou forms of a date obviously more recent as shown by their relatively fresh condition. Perhaps this last argument is not very effective, but certainly that of the mere subspecific differentiation of cave forms from modern ones is to be carefully considered. Would a relationship as close as this be expected between early Pleistocene and recent types? Perhaps, but it is not nearly so likely as between Middle Pleistocene and recent forms.

The correlation of the Yenchingkou deposits and their contained fauna with related cave deposits and faunas and antecedent terrestrial flood plain deposits and their contained faunas in southeastern Asia can be represented as follows¹:

	INDIA	BURMA	YUNNAN	SOUTH CHINA	NORTH CHINA
				Kwangsi caves	
Middle Pleistocene	Boulder Conglomerate	Mogok caves	Hoshantung cave	Yenchingkou pits Tanyang caves	Choukoutien fissures
Lower Pleistocene	Pinjor Tatrot	Upper Irrawaddy	Ma Kai Valley deposits		Nihowan (Sanmen)

NATURE OF THE MATERIAL COMPRISING THE YENCHINGKOU FAUNA

A very perplexing problem arises in connection with a considerable number of the

¹ The lower and middle Pleistocene stages here given are called the Siva-Malayan and Sino-Malayan faunas, respectively, by von Koenigswald (1939, 1940). Further correlations by genera with the Pleistocene faunas of Java will be found in Hooijer (1952).

species assigned to the Yenchingkou fauna. Do the bones from the pits invariably represent animals that were members of the Pleistocene fauna, or do some of them represent intrusions of a later age—animals that have fallen into the pits in subrecent or recent days? In some cases, such as those of the large *Stegodon orientalis* and the giant panda (*Ailuropoda melanoleuca fovealis*), there can be no doubt but that all the material is thoroughly fossil and that the species represented by this material are extinct members of a fauna having an appreciable geologic age. In other cases, however, the question as to whether or not the supposed fossils are actually representative of animals contemporaneous with the true Pleistocene Yenchingkou fauna cannot be so easily answered. Occasionally there seems to be a mixture of material, some thoroughly fossilized, some having the appearance of recent intrusions into the Yenchingkou mammalian assemblage. This is true, for instance, of the badger (*Arctonyx*). In still other cases, such as that of the golden monkey (*Rhinopithecus*), most if not all of the material has a suspiciously recent look. Thus, of the specimens listed as representing *Rhinopithecus roxellanae tingianus*, only one can be classified as showing evidence of having any appreciable geologic age. All the other specimens are of light weight, and the bone is hard and rath-

er elastic—evidences of the fact that there has been little replacement of the original bone. Therefore, it is possible that these specimens represent not animals contemporaneous with *Stegodon* and the other forms that we know are of Pleistocene age, but those of a much later age that fell into the pits, to become mixed in with the older fossils.

Indeed, from the nature of these pits, it

would be surprising if the remains found in them were limited to a single geologic horizon. Many of the pits were, over a considerable period of the Pleistocene, and still are, dangerous traps for unwary animals, so that the accumulation of bones found in them represents an accretion that has been built up from about the beginning of the Middle Pleistocene to the present day.

Of course the fact that some specimens may be more recent than those truly comprising the Yenchingkou fauna does not necessarily mean that they also were not members of that mammalian assemblage, for there is every reason to think that many of the Yenchingkou mammals persisted through the later phases of the Pleistocene and into Recent times. During that period of persistence there may have been changes of a subspecific nature, or it may be that little if any change was involved. That is why a real question is involved in the consideration of certain Yenchingkou forms concerning their specific identity with, and subspecific differentiation from, the corresponding recent animals from this section of China. Cases are individually discussed in the consideration of each form.

It will be noticed that the American Museum collection of Yenchingkou mammals is conspicuously lacking in very small forms, the microfauna. Young (1935a) gives a list of certain insectivores and small rodents, the remains of which had been found in an inspection of the rubbish left by the excavation of two fossiliferous pits at Yenchingkou. As remarked by Young, their age is not certain, since they were not collected *in situ*. However, mixed with the microfauna were a number of fragmentary bones belonging to the large mammals described by Matthew and Granger. Of the forms mentioned in the list below, only *Tamias* and *Pteromys* are stated to be thoroughly fossilized, while the others look rather fresh.

Chiroptera indet.
Sorex cylindrocauda
Anourosorex squamipes
Scaptochirus sp.
Tamias asiaticus
Pteromys cf. *xanthipus*
Eothenomys melanogaster
Apodemus sylvaticus
Rattus rattus

SPECIES AND SUBSPECIES IN FOSSIL MATERIALS

In the discussion of the general aspects of the Yenchingkou fauna presented above an attempt is made to show that the fauna can be divided into several categories, namely, completely extinct genera and species, species belonging to genera not now found in this portion of Asia, and finally forms closely related to the modern species now living in this portion of Szechwan or in closely adjacent regions. In a comparison of the fossil fauna of Szechwan with the recent fauna from the same region, it is obvious that the differences between the two assemblages will be apparent in the first two of the above-named categories, so that in these cases no particular difficulties are encountered during the course of the comparative study. It is in the comparison of fossils with their recent counterparts from the same region that the greatest perplexities connected with this study arise.

The question arises as to whether the supposedly extinct mammals of this category from Szechwan are truly specifically separable from the recent animals found in this region. Matthew and Granger in 1923 designated various fossil types as distinct, and from the very incomplete manuscript on this subject left by Matthew at the time of his death it is apparent that he regarded still other types, not described in the 1923 paper, as new forms specifically separable from their recent relatives.

But in reviewing the fauna, both described and undescribed material, the present writers have doubted whether such distinctions as indicated by Matthew and Granger can truly be drawn. Close morphologic study of the fossils supplemented by extensive comparative measurements have revealed that the bases for separating many of the fossil types from their recent counterparts are at best subtle and usually tenuous. Yet, even so, one gets the impression in working over the material that a difference does exist in most cases between the fossil and recent specimens, even though such a difference is hard to define. In most cases it is apparent that the fossil specimens are in general larger than similar recent types, and this is usually visible in a comparison of the respective

means and modes. But there are strong size overlaps when all the material available is taken into consideration, so that usually a sharp differentiation between the extinct and persisting forms cannot be made. Consequently the question of subspecific distinctions comes to mind—might it not be possible that we are dealing in this case with differences of less than specific magnitude but none the less real?

Subspecific differences among modern mammals are based of course on various criteria, among them morphological differences, differences in the distribution of populations, and the presence of isolating factors that tend to keep populations separated. When fossils are dealt with, however, such factors as range and isolating factors are difficult if not impossible to evaluate; therefore the paleontologist must depend on morphology as his basic criterion for taxonomic separations.

It was thought advisable to investigate briefly and at random, as a sort of sampling study, the problem of subspecific separations as they may be reflected in osteological characters among some modern mammals, to see if such a study would throw any light on the possible relationships of the fossil mammals from Yenchingkou. If subspecific differences

appear in the osteology of modern forms, and if such differences can be distinguished from specific differences as reflected by osteological characters, then perhaps some conclusions can be drawn as to the proper distinctions to be made between the fossils from Szechwan and their modern counterparts from the same region.

In these comparisons the method of ratio diagrams as recently developed by Simpson was utilized. This is a very convenient method of comparing closely related animals, particularly in that it shows the resemblances and differences of a combination of characters. As Simpson has pointed out, "The basic purpose of the diagram is to represent each of a number of analogous observations by a single entry and to plot them in such a way that the horizontal distance between any two of them will represent the ratio of either one of those two to the other" (Simpson, 1941, p. 23). The method is not discussed here; the reader is referred to Simpson's paper. Suffice it to say that various analogous measurements are made on a series of specimens representing two or more forms. The logarithms of the greatest dimension, the least dimension, and the mean for each mensuration category are plotted, and in this way the various measurements can be

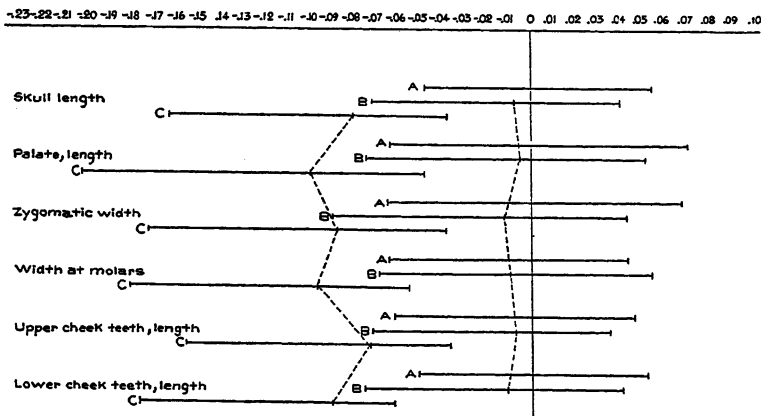


FIG. 2. Ratio diagram showing comparison of certain osteological characters in two species of *Mustela* and two subspecies of *Mustela sibirica*. The latter show a strong overlap of the characters measured, whereas the two species of *Mustela* show little overlap in these same characters. A. *Mustela sibirica fontanierii*, six males, four females. B. *Mustela sibirica davidiana*, six males, three females. C. *Mustela altaica kathiak*, four males, three females, one indeterminate. Data from Allen, 1938.

compared with one another and the forms being studied can also be compared one with another to great advantage.

The first comparison was made between two subspecies of *Mustela*, as based on material presented in Glover Allen's monograph on the recent mammals of China (Allen, 1938, pp. 371-381). The two forms, *Mustela sibirica fontanierii* and *Mustela sibirica davidiana*, the former based on a series of 10 individuals (six males and four females), the latter on nine individuals (six males and three females), were compared as shown in figure 2. The interesting fact, at once apparent in this comparison, is that there is a very strong overlap between the two subspecies in all the osteological characters considered—so much so that one might wonder on this basis alone as to the validity of any real subspecific separation between them. Yet their ranges are quite separate and do not overlap, the former being a North Chinese type of Palearctic distribution, the latter a southwestern Chinese type of Oriental distribution.

To carry this study still further, a distinct species, *Mustela altaica kathiah*, represented by a series of eight individuals (four males, three females, and one of unknown sex),

was compared with the two subspecies just discussed. It can be seen from the ratio diagram (fig. 2) that the means of this form, which is supposedly specifically distinct from the two forms mentioned above, show a wide separation from the means of the two subspecies of *Mustela sibirica*, with a certain amount, but a relatively small proportion, of overlap. Consequently, if the specific and subspecific separations of these Chinese mustelids are correct, it would seem that, so far as morphology is concerned, subspecific distinctness, based as it is for the most part on external characters, shows little differentiation in the measurable osteological characters, while specific distinctness, being of a more deep-seated nature, is apparent in the osteological characters.

To check this general picture of the close osteological relationships between subspecies, a second ratio diagram (fig. 3) was drawn up for two subspecies of the big-eared rat of the Congo, as discussed by Hatt (Hatt, 1940, pp. 502-503). Here again, it can be seen that there is a strong overlap in osteological characters between two subspecies in all but one character, that of the size of the bullae. This diagram was based on relatively

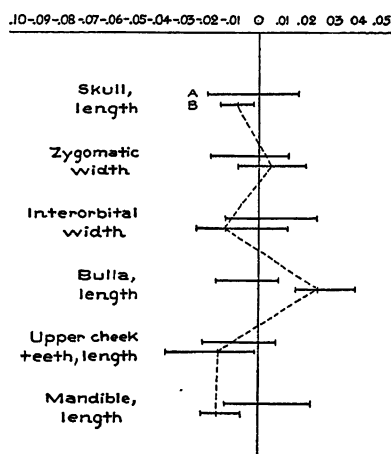


FIG. 3. Ratio diagram showing comparison of certain osteological characters in two subspecies of *Malacomys longipes*. This diagram shows a strong overlap of the characters measured, except for the length of the bulla. A. (Upper bar.) *Malacomys longipes centralis*, five males. B. (Lower bar.) *Malacomys longipes wilsoni*, five males. Data from Hatt, 1940.

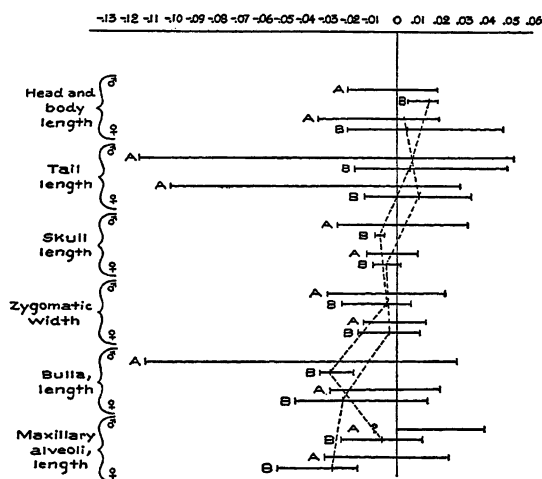


FIG. 4. Ratio diagram showing comparison of certain osteological characters in two subspecies of *Funisciurus congicus*. The sexes are separately plotted. A strong overlap in the measured characters is evident. A. *Funisciurus congicus flavinus*, nine males, 34 females. B. *Funisciurus congicus congicus*, four males, eight females. Data from Hill and Carter, 1941.

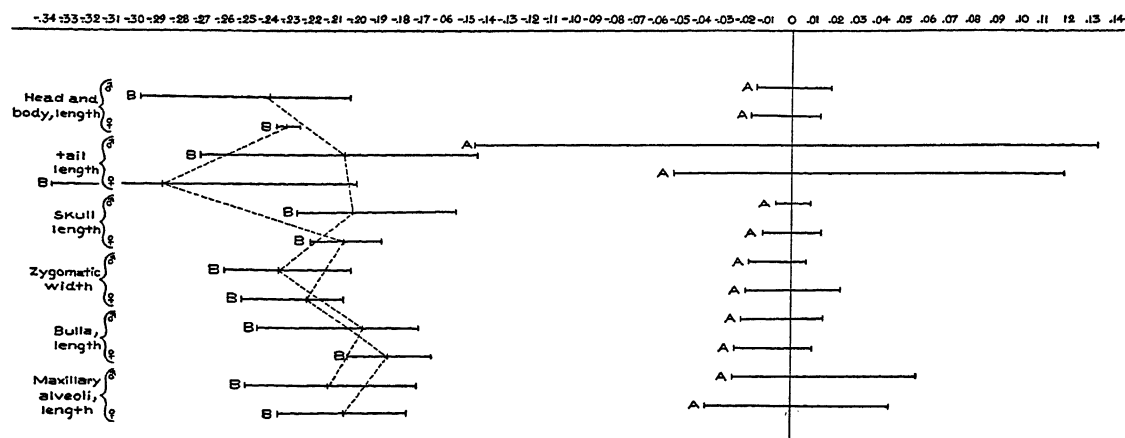


FIG. 5. Ratio diagram showing comparison of certain osteological characters in two species of *Cryptomys*. There is virtually no overlap in the characters measured. A. *Cryptomys mechowii*, six males, six females. B. *Cryptomys bocagei*, 10 males, five females. Data from Hill and Carter, 1941.

small suites of specimens, five males in each case, so a third check was deemed desirable.

This was found in a comparison of two subspecies of the genus *Funisciurus*, discussed by Hill and Carter in their monograph of the mammals of Angola (Hill and Carter, 1941, pp. 70-73). In this case fairly large suites were available—43 individuals of *Funisciurus congicus flavinus* and 12 of *Funisciurus congicus congicus*. The ratios between sexes are rather uneven; in the former of the above-mentioned types there were nine males and 34 females, while in the latter there were four males and eight females. In the ratio diagram the various osteological characters for the sexes were separately plotted. Again, the strong overlap in osteological characters between subspecies can be seen. The few apparent aberrations in this diagram are probably due to the disparities in the sizes of the samples compared, so it might be expected that with suites of more nearly equal size such divergences would tend to disappear. But with all these qualifications taken into account, it is still apparent that the overlap in these subspecies is very strong indeed.

After the very close osteological relationships between subspecies was checked, in several cases by an application of the ratio diagram method, an additional test was made of the seeming distinctness of osteological characters between truly recognizable species.

For this purpose the data published by Hill and Carter (Hill and Carter, 1941, p. 200) on the genus *Cryptomys* from Angola were utilized. In this case, two distinct species were compared, *Cryptomys mechowii* and *Cryptomys bocagei*, and, as may be seen in figure 5, they show virtually no overlap in osteological or proportional characters, the only overlap whatsoever in this case being in one highly variable character, namely, the length of the tail. Otherwise the two species are quite distinct and separate.

From the above considerations it seems evident that in many cases the differences between closely related species and subspecies can be detected by comparisons of osteological measurements, especially by an application of the ratio diagram method. Perhaps species and subspecies relationships can be expressed in a general way as follows.

Closely related species may show little overlap of quantitative osteological characters, for the differences between forms of this taxonomic rank are sufficiently deep-seated to be reflected in the size and proportions of the skeleton. Closely related subspecies, on the other hand, may show a very strong overlap of their quantitative osteological characters, since the differences between forms of this taxonomic rank are for the most part not sufficient to be strongly indicated by size differences in the skeletal parts. However, even where there is a strong overlap of quan-

titative osteological characters, there may be significant differences in the means of these characters.

ACKNOWLEDGMENTS AND ABBREVIATIONS

We wish to acknowledge the work done by several artists and photographers in making illustrations for this paper. Line drawings of specimens, except those of *Stegodon*, were made by Mr. John C. Germann. The drawings of proboscideans were taken from Osborn's monograph on the Proboscidea, published by the American Museum of Natural History. The map and the various diagrams and charts were made by Mrs. Elsa Arnoux. The photographs of specimens were made by the photographic division of the American Museum of Natural History.

The junior author wishes to express his sincere appreciation to the Director and staff of the American Museum of Natural History for the help and facilities given to him during his stay at the Museum, from the spring of 1950 to the fall of 1951.

The names of various institutions are ab-

breviated when used in connection with the official catalogues of those institutions, as follows:

A.M.N.H., the American Museum of Natural History, Department of Geology and Paleontology

A.M.N.H.(C.A.), the American Museum of Natural History, formerly Department of Comparative Anatomy, now under the jurisdiction of the Department of Mammals

A.M.N.H.(M), the American Museum of Natural History, Department of Mammals

B.M., British Museum (Natural History)

C.N.H.M., Chicago Natural History Museum

U.C.M.P., University of California, Museum of Paleontology, Berkeley

U.S.N.M., United States National Museum

The following abbreviations are used in the tables:

a, approximate measurement

e, estimated measurement

L, length

Los, length, outer surface

W, width

Wa, width, anterior diameter

Wp, width, posterior diameter

SYSTEMATIC DISCUSSION OF THE YENCHINGKOU FAUNA

PRIMATES

CERCOPITHECIDAE

RHINOPITHECUS MILNE-EDWARDS

Rhinopithecus A. MILNE-EDWARDS, 1872, Recherches pour servir à l'histoire naturelle des mammifères, p. 233.

GENERIC TYPE: *Semnopithecus roxellanae* A. Milne-Edwards.

DIAGNOSIS: Nose prominent and upturned, humerus longer than forearm, limbs less slender than in langur monkeys, more nearly equal to each other in length, tail relatively shorter. Skull with smoothly rounded braincase, reduced nasal bones, and large nasal aperture. Teeth rather broad.

Rhinopithecus roxellanae tingianus

Matthew and Granger

Rhinopithecus tingianus Matthew and Granger, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 588.

TYPE: A.M.N.H. No. 18466, skull of a subadult individual with the milk molars and the first two permanent molars.

PARATYPES: A.M.N.H. Nos. 18467, portion of a left maxilla with P^4-M^2 ; 18468, right maxilla with P^4-M^3 ; 18469, left mandibular ramus with P_4-M_3 .

REFERRED SPECIMENS: A.M.N.H. Nos. 18746, right maxilla with P^3-M^2 ; 21788, left maxilla with P^4-M^1 .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: "Larger and more robust throughout than *R. roxellanae*. Size about as in *R. bieti* but with much smaller teeth" (Matthew and Granger, 1923, p. 588).

DISCUSSION

The presence of *Rhinopithecus* (the golden monkey) at Yenchingkou is indicated by a very fine skull of a subadult (?) male, and in addition several maxillary fragments and the portion of a lower jaw. This occurrence is considerably to the east of the range typical of present-day golden monkeys, although it is not very far in a northeast direction from the supposed range of *Rhinopithecus brelichi* (a modern "species," of which one specimen, the type, is known, and for which the type locality is not at all definitely determined).

At any rate, the presence of *Rhinopithecus* at Yenchingkou probably represents a former eastward extension of the range for this monkey, and suggests the possibility that the separated ranges of the modern "species" may be the remnants of an earlier, continuous distribution extending over a greater portion of the province of Szechwan.

Matthew and Granger distinguished the remains from Yenchingkou as "larger and more robust throughout than *R. roxellanae*." A comparison with the recent species does not exactly bear out this supposed distinction. In fact, a subadult male specimen of *R. roxellanae* in the United States National Museum (No. 258986) in identically the same stage of development as the fossil skull, that is, with the sutures of the skull well delineated, the milk molars still present but the permanent incisors erupted, and with the third molar unerupted, is practically identical in size with the Yenchingkou specimen. In the American Museum of Natural History is a *Rhinopithecus* skull of a female in almost the same stage of development, that is, the permanent premolars are already in place but the third molar is still unerupted, and this specimen is distinguished from the fossil, as well as from the recent male, by the somewhat narrower palate, the more constricted anterior portion of the dental arch, and the narrower nasal aperture. From the broad palate, showing particularly a relatively greater breadth in the canine region, from the presumably heavier nose, and also from the slightly larger teeth and somewhat heavier orbital ridges in the fossil and the recent male as compared with the female, there is every reason to think that the fossil skull represents a male individual. All the differences that can be found are well within what might be expected as the range of individual variation.

The four maxillary fragments come from fully adult individuals and do not bear out the statement by Matthew and Granger that *Rhinopithecus tingianus* is a form larger and more robust than *Rhinopithecus roxellanae*. As will be seen from table 4 in which the tooth measurements of these fossil specimens are compared with those of a series of 11 recent skulls there is no difference in size of the

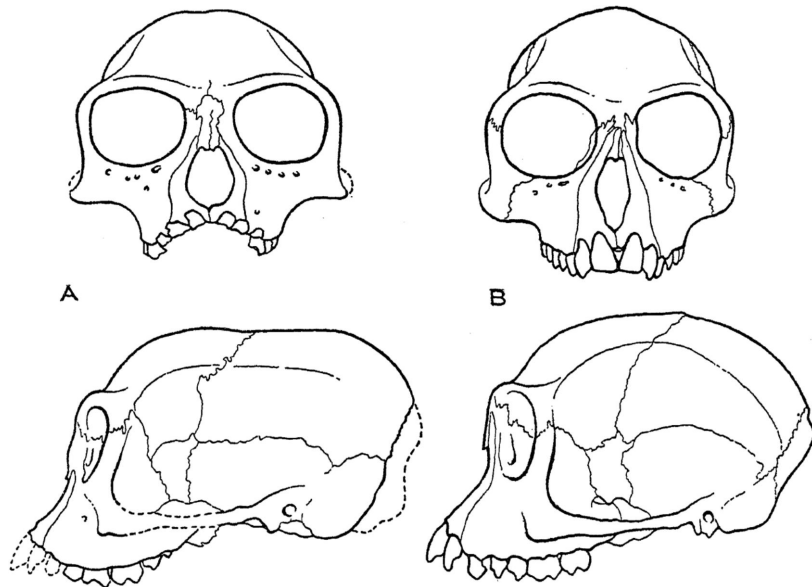


FIG. 6. A. *Rhinopithecus roxellanae tingianus* Matthew and Granger. Type, A.M.N.H. No. 18466, skull of subadult with milk molars and first two permanent molars. Anterior and left lateral views. B. *Rhinopithecus roxellanae roxellanae* Milne-Edwards. A.M.N.H. No. 110456, skull of adult. Anterior and left lateral views. All figures one-half natural size.

molars. The size difference shows only in the mandible A.M.N.H. No. 18469, which is not only deeper at M_1 than any of the recent mandibles used for comparison but also has teeth which are above the maximum size as found for the recent golden monkey.

The difference in size between the fossil and the recent *Rhinopithecus roxellanae* is not great, but evidently we have a form that is larger, on the average, than the recent example belonging to the same species. We propose to reduce the status of the fossil Szechwan form, *Rhinopithecus tingianus* Matthew and Granger, to that of a subspecies of the recent *Rhinopithecus roxellanae* (A. Milne-Edwards). As already noted above, the occurrence of *Rhinopithecus roxellanae tingianus* is beyond that of the recent subspecies also geographically.

No fossil remains of *Rhinopithecus* have been recorded thus far from any locality beyond Yenchingkou. Since the genus is also present in Indo-China (Dollman, 1912), fossil remains can be expected to be found some day in this general area also.

HYLOBATIDAE

BUNOPITHECUS MATTHEW AND GRANGER

Bunopithecus MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 588.

GENERIC TYPE: *Bunopithecus sericus* Matthew and Granger.

DIAGNOSIS: "Generic Distinctions.—Jaw and teeth much as in *Hylobates* except for greater width of molar and large size of hypoconulid on m_2 and m_3 " (Matthew and Granger, 1923, p. 588).

Hylobates (Bunopithecus) sericus (Matthew and Granger)

Bunopithecus sericus MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 588.

TYPE: A.M.N.H. No. 18534, a lower jaw with M_{2-3} on the left side.

PARATYPES: None.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: See the generic diagnosis above.

TABLE 3
SKULL MEASUREMENTS (IN MILLIMETERS) OF FOSSIL AND RECENT
Rhinopithecus roxellanae

	<i>R. r. tingianus</i> A.M.N.H. No. 18466 ♂?	<i>R. r. roxellanae</i> U.S.N.M. No. 258986 ♂	A.M.N.H. (M.) No. 110456 ♀
Length, premaxillary to external auditory meatus	72	69	72
Width, parietals	68	69	64
Width, orbits	24	26	25
Vertical diameter, orbits	21	24	22
Width, nasal aperture	12.5	13	9
Length, basal bones	13.5	11.5	11
Width, palate at M ¹	21.5	20	17.5
M ¹ , L×W	7.3×7.8	8.8×8.1	8.1×7.8
M ² , L×W	9.0×9.0	9.8×9.7	9.0×8.9

DISCUSSION

Hylobates (Bunopithecus) sericus is a rather large gibbon, about equal in size, as Matthew and Granger have pointed out, to the recent hoolock. Unfortunately the type specimen, and to date the only known fossil, is a fragment of a lower jaw, which may prove to be less definitive than it was thought to be by the authors of this form. Matthew and

Granger distinguish *Bunopithecus sericus* from the gibbon by reason of the greater (relative) width of the molars in the fossil, the large size of the hypoconulid in the fossil, and the fact that the talonid is broader than the trigonid and M₃ is broader than M₂ in the fossil.

None of these differences will hold if *Bunopithecus* is compared with a series of modern

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF TEETH OF FOSSIL AND RECENT *Rhinopithecus roxellanae*

	M ¹		M ²		M ³		M ₁		M ₂		M ₃		Depth of Ramus at M ₁
	L	W	L	W	L	W	L	W	L	W	L	W	
<i>R. r. tingianus</i>													
A.M.N.H. No. 21788	8.5	7.9	—	—	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 18467	7.8	7.5	8.9	9.1	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 18468	7.9	7.4	8.7	9.0	8.6	8.7	—	—	—	—	—	—	—
A.M.N.H. No. 18746	7.2	7.3	8.1	8.6	—	—	—	—	—	—	—	—	—
A.M.N.H. No. 18469	—	—	—	—	—	—	7.6	7.5	9.3	8.2	12.5	8.1	30.5
<i>R. roxellanae</i>													
U.S.N.M. No. 268887, ♂	7.8	7.7	8.8	9.3	9.0	9.0	7.8	6.5	9.3	7.5	10.6	7.1	27.0
U.S.N.M. No. 268886, ♀	7.9	7.3	9.0	8.7	9.4	8.8	7.4	6.3	8.6	7.7	11.3	7.6	23.5
U.S.N.M. No. 268888, ♀	7.5	7.2	8.8	8.5	8.0	8.4	7.1	6.0	8.6	7.0	9.6	6.9	20.0
U.S.N.M. No. 268890, ♀	7.6	7.7	8.8	9.3	8.8	9.3	7.4	6.7	9.3	7.8	11.7	6.9	21.5
U.S.N.M. No. 268891, ♀	8.0	7.2	8.8	8.6	7.6	8.3	7.6	6.2	8.5	7.1	10.4	7.0	23.5
U.S.N.M. No. 268892, ♀	7.5	7.5	8.7	8.8	7.5	8.4	7.2	6.1	8.6	6.8	10.1	6.8	20.0
U.S.N.M. No. 268893, ♀	7.8	7.6	8.3	8.7	8.6	9.0	7.1	6.4	8.4	6.8	10.5	7.3	19.5
U.S.N.M. No. 268894, ♀	8.0	7.2	8.6	8.3	8.8	8.4	7.5	6.2	8.8	7.3	10.3	7.4	20.5
U.S.N.M. No. 268895, ♀	7.8	7.4	9.0	8.8	8.4	8.7	—	6.4	—	7.4	10.6	7.5	22.5
U.S.N.M. No. 268897, ♀	7.8	7.4	8.8	8.6	8.7	8.8	7.4	6.0	8.6	6.8	10.6	7.2	20.5
A.M.N.H. (M.) No. 119648, ♀	8.6	7.8	9.5	9.1	9.0	8.4	8.0	6.8	9.2	7.3	11.5	7.8	19.5

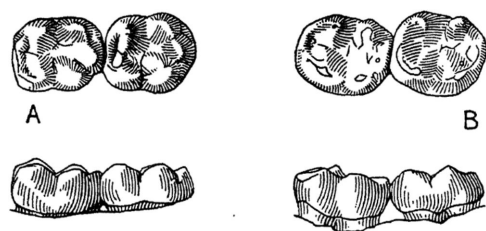


FIG. 7. A. *Hylobates* (*Bunopithecus*) *sericus* Matthew and Granger. Type, A.M.N.H. No. 18534, left M_{2-3} . Crown and lateral views. B. *Hylobates* sp. A.M.N.H. (C.A.) No. 549, left M_{2-3} . Crown and lateral views. All figures one and one-half times natural size.

gibbons, where specific differentiation and individual variation are taken into account. Thus among a number of gibbon jaws, chosen at random, it was found that generally speaking the molars were about the same as those of *Bunopithecus* as regards relative width, and that some were even relatively broader in the modern representatives than they are in the fossil. In some of the modern gibbon jaws the hypoconulid is very large, fully as large as the entoconid, so this character cannot be used in making a valid separation of the fossil form from the modern genus, *Hylobates*. Furthermore, in some modern specimens the talonid of the lower molars is broader than the trigonid just as is the case in the fossil. And the last molar in the modern

Hylobates is often comparable to the second molar in size and width. Remane (1921, p. 27), who examined 115 skulls of various *Hylobates* species, states that M_3 is the largest in the lower molar series in 30.5 per cent of the specimens.

Consequently it does not seem possible to separate the fossil from the modern gibbons. While *Hylobates* (*Bunopithecus*) *sericus* is probably a distinct species, it is almost certainly not separate generically from *Hylobates*. A solution of this problem must await the discovery of additional fossil material.

The presence of *Bunopithecus* at Yenching-kou is interesting zoogeographically in that it extends the range of the gibbons in the Pleistocene beyond that of their present-day distribution. The modern gibbons range through Indo-China, Sumatra, Borneo, and adjacent regions, reaching as far north as the western border of Yunnan on the west and the Island of Hainan and the adjacent coastal regions on the east.

LAGOMORPHA

LEPORIDAE

LEPUS LINNAEUS

Lepus LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 57.

GENERIC TYPE: *Lepus timidus* Linnaeus.

DIAGNOSIS: Skull with short bony palate;

TABLE 5
MEASUREMENTS (IN MILLIMETERS) OF LOWER MOLARS OF GIBBONS

	<i>Hylobates</i> (<i>Bunopithecus</i>) <i>sericus</i> A.M.N.H. No. 18534	<i>Hylobates</i> sp. A.M.N.H.(C.A.) No. 549	<i>Hylobates</i> sp. A.M.N.H.(M.) No. 63591	<i>Hylobates</i> sp. A.M.N.H.(M.) No. 2513
M_2				
L	7.1	8.1	7.4	5.7
W	6.2	6.9	6.3	5.5
Index	87	85	85	96
M_3				
L	7.5	7.6	6.9	6.2
W	6.5	6.8	6.1	5.2
Index	86	89	88	84
Depth of ramus at M_3	14.4	14.8	14.5	12.4
Ratio: M_3 length/depth of ramus	52	51	47	50

postorbital processes broad and triangular. Cheek teeth hypsodont, without roots, and prismatic. Hind legs and ears very long.

Lepus sp.

SPECIMEN UNDER CONSIDERATION: A.M.N.H. No. 18418, a left mandibular ramus with P_3 - M_2 ; incisor and ascending ramus missing.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DISCUSSION

This single specimen represents a possible addition to the extinct fauna of Yenchingkou. Because of the unfossilized appearance of the bone, it is quite possible, however, that

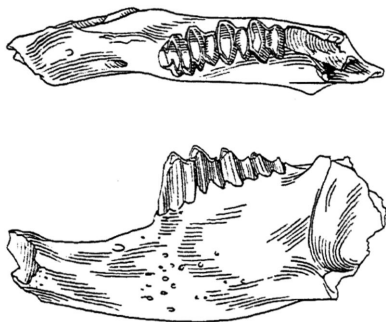


FIG. 8. *Lepus* sp. A.M.N.H. No. 18418, left mandibular ramus with P_3 - M_2 . Crown and lateral views. One and one-half times natural size.

the specimen indicates a recent or subrecent animal that had fallen into one of the pits, to be included in the general mixture of mammalian remains at the bottom. This is a small or medium-sized hare, more or less comparable to, but perhaps smaller than, *Lepus europaeus* or *Lepus oiostolus*, still persisting in Szechwan, or *Lepus wongi*, described by Young from Choukoutien and other Pleistocene localities of similar age. Its measurements (in millimeters) are as follows: length of P_3 - M_2 , 11.1; depth of ramus at P_4 , 12.9, length of M_1 , 2.9; width of M_1 , 3.7.

RODENTIA

RHIZOMYIDAE

RHIZOMYS GRAY

Rhizomys J. E. GRAY, 1831, Proc. Zool. Soc. London, no. 8, p. 95.

GENERIC TYPE: *Rhizomys sinensis* Gray.

DIAGNOSIS: A robust rodent, with large incisors having orange-colored enamel, and rooted molars with reentrant folds. No premolars.

Rhizomys sinensis troglodytes

Matthew and Granger

Rhizomys troglodytes MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 574-576.

TYPE: A.M.N.H. No. 18408, a skull.

PARATYPES: A.M.N.H. Nos. 18401, front of skull; 18402a-c, two good skulls, one front of skull; 18403, front of skull; 18404, right jaw; 18405a-j, 10 partial skulls; 18406a-d, four partial skulls; 18407a-f, six partial skulls; 18409a-z, aa-gg, 33 incomplete skulls, of which 18409a, 18409r, and 18409aa have associated lower jaws; 18410a-t, 20 jaws; 18411, front of skull; 18412a-i, nine partial skulls; 18413a-d, four partial skulls; 18414, skull; 18415a-b, two partial skulls; 18416a-f, five partial skulls and one, 18416f, almost complete with associated lower jaws; 18417a-d, four partial skulls, of which 18417a has associated lower jaws.

REFERRED SPECIMENS: A.M.N.H. Nos. 18399, front of skull; 18400, right jaw; 18427, jaw fragment; 18506a-i, nine jaws, three almost complete; 18585, partial right jaw; 18586a-b, two partial jaws; 18587a-n, six almost complete, eight partial, jaws; 18588a-l, one complete, 11 partial jaws; 18589a-h, eight partial jaws; 18590a-i, nine partial jaws; 18591a-z, 16 almost complete, 10 partial, jaws; 18592a-z, 10 almost complete, 16 partial, jaws; 18593a-z, 11 almost complete, 15 partial, jaws; 18594a-z, nine almost complete, 17 partial, jaws; 18595a-d, four jaws; 18596a-j, 10 jaws; 18597a-g, two complete, five partial, jaws; 18598a-d, four jaws; 18599, a partial jaw; 18600a-b, two partial jaws; 18766a-c, three partial skulls; 18767a-b, two partial jaws; 18768a-g, seven jaws; 18769a-h, two almost complete, six partial, skulls; 18770a-j, five complete, five partial, skulls; 18771a-m, 13 jaws; 18772a-l, 12 jaws; 18773, incomplete skull; 18774, front of skull; 18775, left jaw; 18776a-c, three partial skulls; 18777, associated skull and lower jaws; 18778, associated skull and lower jaws.

HORIZON AND LOCALITY: Pleistocene; Yen-chingkou, Szechwan, China.

DIAGNOSIS: "Distinctive Characters.—(a) Size large, length of skull incisors to condyles = 77–85 mm.; (b) skull rather long and narrow, postorbital crests contracting sharply behind the orbits to a long and well-marked sagittal crest; (c) infra-orbital foramen subtriangular, the maxillary crest in front of it and plate beneath extended upward on the side of the muzzle almost to its upper surface; (d) nasals long, narrow, wedge-shaped, tapering backwards almost to a point; (e) squamosals fail to reach the sagittal crest superiorly or the postorbital constriction anteriorly; (f) occiput strongly sloped forward; (g) posterior nares narrow and contracted transversely; (h) bulla somewhat flattened inferiorly, strongly convex anteriorly, culminating in a ridge directly behind the posterior [median?] lacerate foramen, slightly reflexed on the anterior inner border against the basisphenoid; (i) carotid foramen lying close behind the basisphenoid-basisoccipital suture and the bulla extending a considerable distance in front of it; (j) bulla strongly reflexed posteriorly upon the surface of the paroccipital process; (k) inferior surface of auditory meatus strongly concave both ways, without any longitudinal ridge, and the opening large and flaring; (l) incisors strongly convex, the points of the upper pair directed somewhat backward, the anterior faces of the lower pair strongly flattened, of the upper pair, moderately so; (m) first upper molar somewhat, and first lower molar considerably reduced and m^1 wearing to a lower grinding plane than the others; (n) third upper molar unreduced, approximately equal to m^2 in size, the posterior portion of the third lower molar correspondingly enlarged and broadened" (Matthew and Granger, 1923, p. 574).

DISCUSSION

Rhizomys sinensis troglodytes is a large bamboo rat, known from a particularly fine series of skulls, jaws, and portions of skeletons collected by Granger at Yen-chingkou. The list of supposedly distinctive characters quoted above was presented by Matthew and Granger in their original description of this form, but unfortunately almost all

these characters are common to the genus. Qualitatively, *Rhizomys sinensis troglodytes* is remarkably similar to *Rhizomys sinensis vestitus*, the recent bamboo rat from Szechwan. Both forms are very closely comparable in size and in the general aspect of their osteological features. There are minor differences, to be sure, the most noticeable being the smaller cheek teeth in the fossil form as well as the lesser vertical diameter of the infraorbital foramen.

Since a large series of the fossils was at hand, it was decided to make simple statistical studies in an effort to determine how this supposedly separate form might be distinguished from recent representatives of *Rhizomys sinensis*, whether the material at hand represents a homogeneous or a heterogeneous group, whether there might be bimodality within the series owing to sexual dimorphism, and the like. Measurements were made of the skulls and jaws (tables 6, 7) and these were interpreted statistically (figs. 10–13).

From the interpretation of the data it is obvious that the specimens of *Rhizomys* from the pits at Yen-chingkou represent a single species, showing a considerable range of size variation, roughly about equal to the combined size ranges of two modern forms, *R. sinensis vestitus* and *R. sinensis davidi*. It may be assumed that anyone having only a few isolated specimens representative of the largest and the smallest individuals of this present series would be inclined to assign them to separate categories, yet a graph of the complete series shows that the specimens fall into a sequence of size groupings that follows a fairly normal curve of variability. Moreover, those measurements that are most numerous give the most normal curve, a still further proof as to the homogeneity of the material. Finally, the curves, from their nature, show that there is no splitting or bimodality due to sexual dimorphism, although in one case (that of the lower jaws) there is a hint of bimodality due to the presence of juvenile and adult specimens in the series.

It is particularly interesting that the type specimen of *Rhizomys troglodytes* is not at all typical as regards those quantitative characters susceptible to statistical analysis, because in each series of measurements

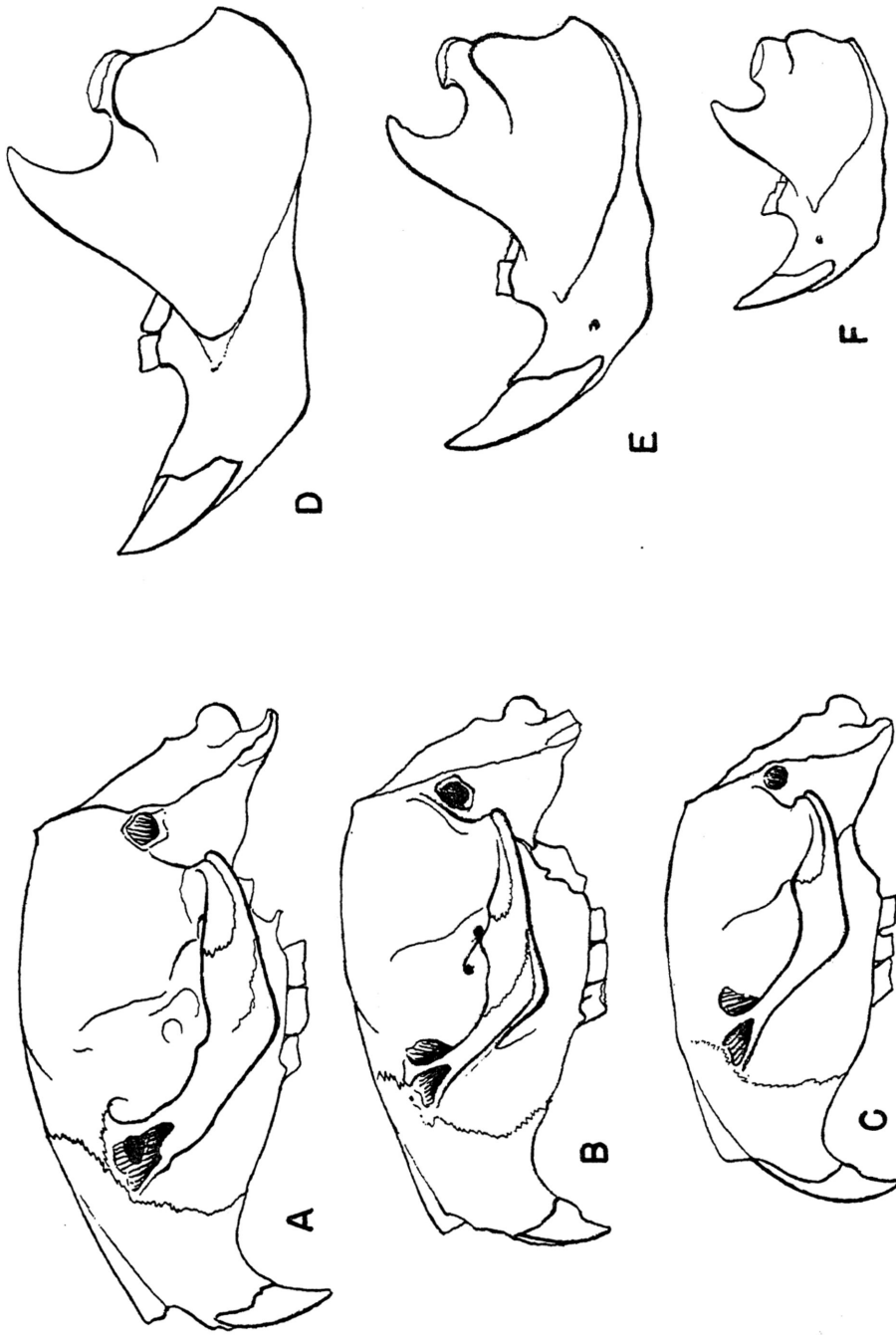


FIG. 9. *Rhizomys sinensis troglodytes* Matthew and Granger. Skulls and mandibles, showing variations in size. A. A.M.N.H. No. 18408, type. B-F. Paratypes. B. A.M.N.H. No. 18770f. C. A.M.N.H. No. 18405a. D. A.M.N.H. No. 18591z. E. A.M.N.H. No. 18771k. F. A.M.N.H. No. 18591v. Left lateral views. All natural size.

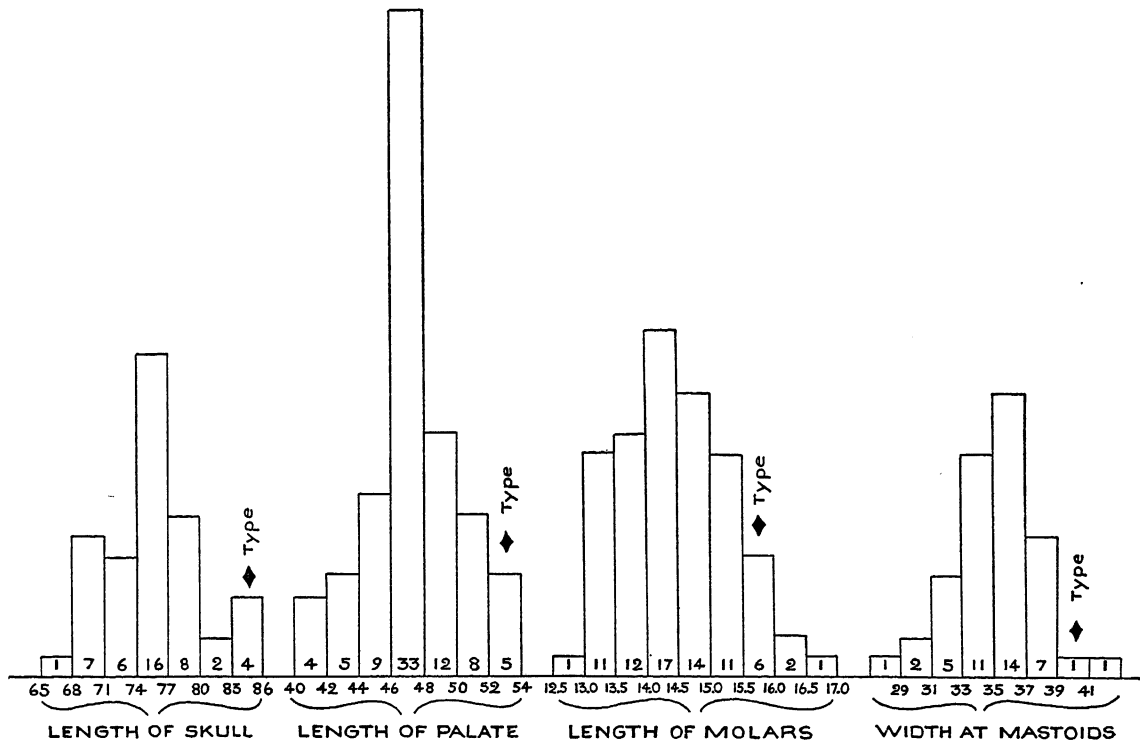


FIG. 10. Histogram of skull measurements of *Rhizomys sinensis troglodytes*.

studied the type occupies a position quite removed from the mean, the mode, and the median for the species. Thus, as can be seen from figure 10, the type is a very large specimen, included in the higher or highest frequencies of each group of measurements.

If the analysis is carried to a comparison with certain recent forms of *Rhizomys*, it can be seen that the Yenchingkou form, as based on a large suite of specimens, is a large member of the genus, comparable in this respect to the modern *Rhizomys sinensis vestitus* living in Szechwan. For instance, the modal length for the skull of the fossil is the same as that for the recent animal mentioned above, while the modal length for the palate of the fossil is but little different from that for the recent type. It is to be noted, however, that the skull of the Yenchingkou *Rhizomys* is relatively narrow compared with the skull of a recent *Rhizomys* having longitudinal dimensions similar to those of the fossil, although the difference is not very great. This was a character noted by Matthew and Granger, and it is the only

character among those mentioned by these authors that is distinctive for the *Rhizomys* from the Yenchingkou pits. One other character, however, seems to separate the fossil form from recent types; in spite of its large size it does not have large teeth. For instance, the modal length for the cheek teeth of the fossil is much less than that for the teeth in the modern *Rhizomys* from Szechwan, this latter being comparable to the fossil in its general size. On the other hand, the modal length of the teeth in the Yenchingkou *Rhizomys* is closely comparable to that for the recent form, *Rhizomys sinensis davidi* from Fukien, an animal considerably smaller than the fossil in general size.

It often happens that comparisons of ratios or indices are useful in arriving at the resemblances or differences that may exist between related animals. When this procedure is applied to the fossil and recent *Rhizomys* here under consideration, certain interesting points come to light.

Thus the ratio between the length of the molar teeth and the length of the skull is

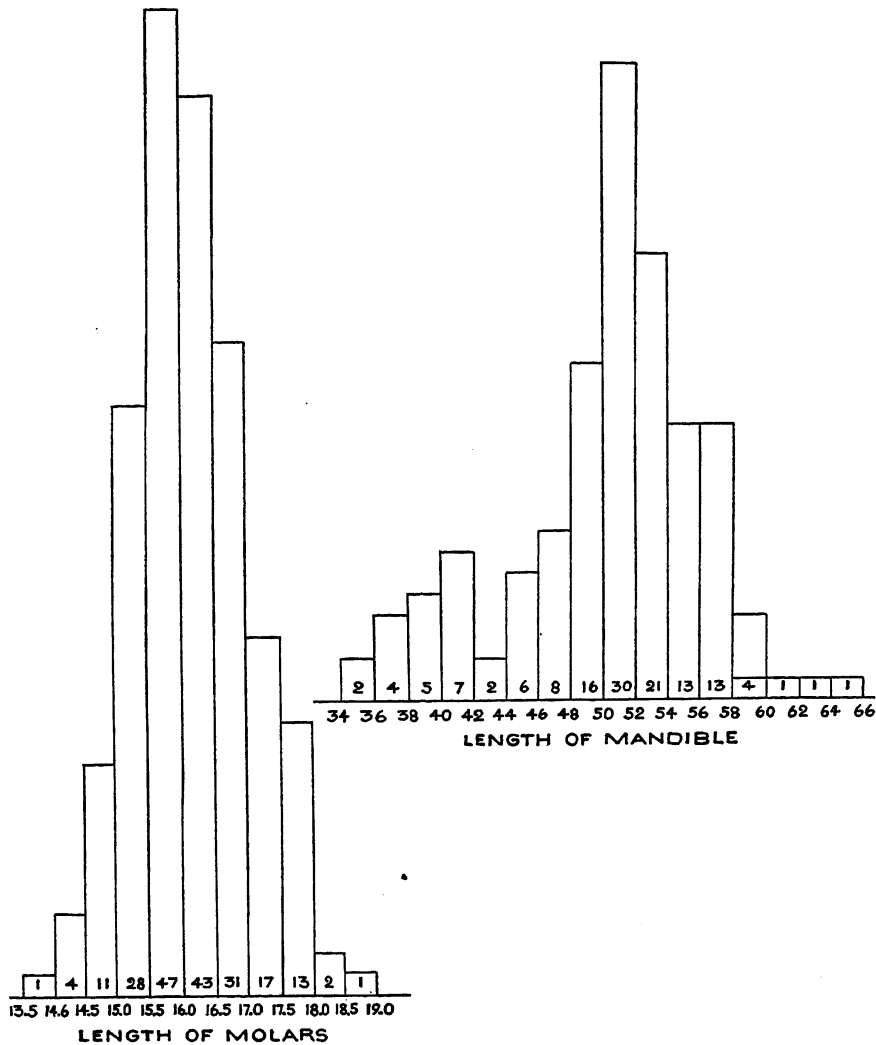


FIG. 11. Histogram of measurements of length of molars and length of mandible in *Rhizomys sinensis troglodytes*.

definitely lower for the Yenchingkou *Rhizomys* than it is for modern types of this rodent—an expression, of course, of the relatively small teeth in the fossil. Again, the ratio of mastoid breadth to skull length is low for the Yenchingkou *Rhizomys*, as compared with the recent bamboo rat from Szechwan—in this case being more or less comparable to the same ratio in the small *R. sinensis davidi*. But other ratios in the forms under consideration, such as the ratio between the zygomatic breadth and the skull length, are fairly constant, showing that the differences in the skull are at best but slight

in these various recent and fossil *Rhizomys*.

On the basis of the resemblances and differences discussed above, it is hereby suggested that the fossil *Rhizomys* from the limestone fissures at Yenchingkou is not a separate species, as originally described by Matthew and Granger, but a subspecies of the modern *Rhizomys sinensis*. An examination of the data and the graphs presented here will show that those differences that served to distinguish the Yenchingkou *Rhizomys* from the modern types are approximately of the same order as the differences separating the several subspecies of *Rhizomys*

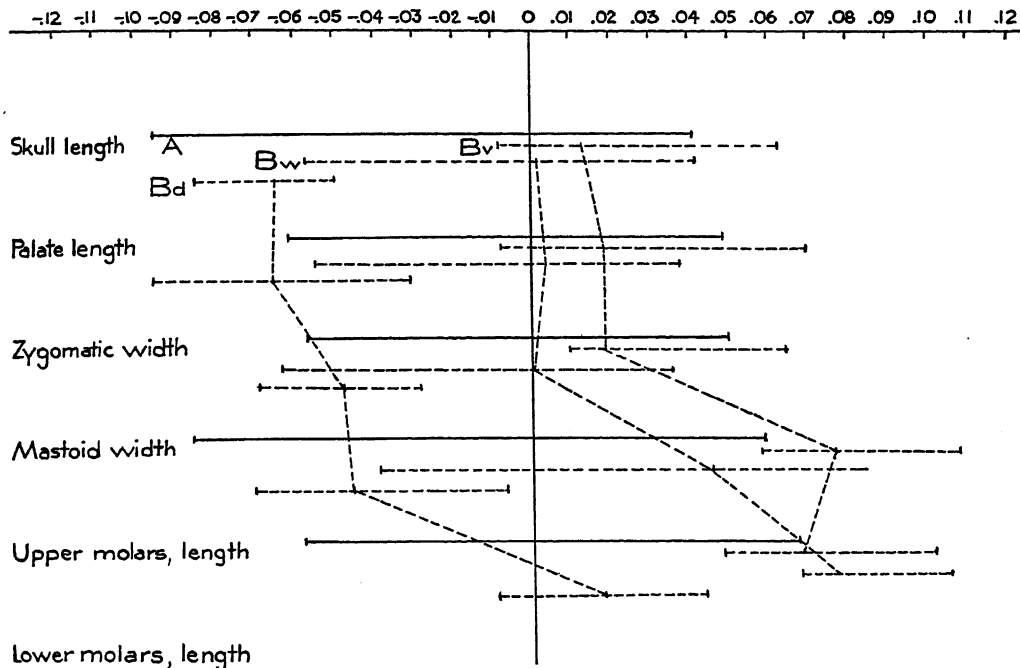


FIG. 12. Ratio diagram comparing range of size variation in *Rhizomys sinensis troglodytes* and three Recent subspecies of *Rhizomys sinensis*. A. *Rhizomys sinensis troglodytes*. Bd. *Rhizomys sinensis davidi*. Bv. *Rhizomys sinensis vestitus*. Bw. *Rhizomys sinensis wardi*.

sinensis. Indeed the Yenchingkou *Rhizomys* is strikingly similar in its osteological and dental features to the modern *Rhizomys sinensis vestitus* from Szechwan, and it is only by the study of certain statistical data based on suites of specimens that those differences that do exist between the extinct and the recent form are made apparent.

Certain unknowns are difficult to evaluate. Thus among the recent bamboo rats the external differences in the color, markings, and texture of the fur are far more striking than correlative differences in the osteological features. Naturally this is a common phenomenon in the study of recent mammals belonging to a single genus, but it is particularly marked in the case of *Rhizomys*. So it is possible that if one could journey back through time to see *Rhizomys sinensis troglodytes* alive, its differences from the surviving forms would be more apparent than they are from a study of osteological material alone. It is probable, however, that such would not be the case, for the very close resemblance between the skull and

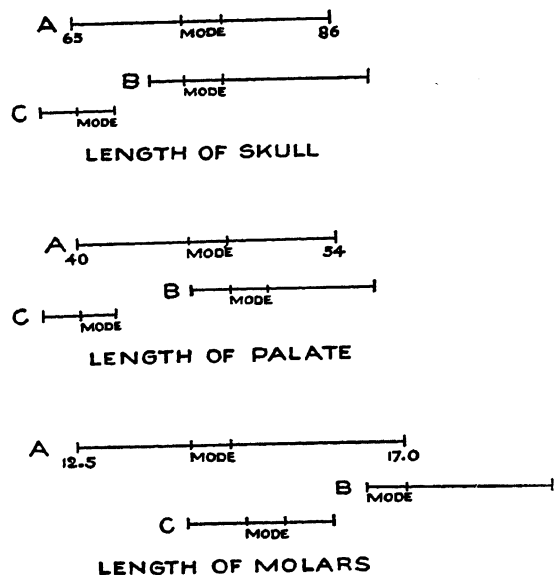


FIG. 13. Diagram comparing length of skull, length of palate, and length of molars in three subspecies of *Rhizomys sinensis*. A. *Rhizomys sinensis troglodytes*. B. *Rhizomys sinensis vestitus*. C. *Rhizomys sinensis davidi*.

TABLE 6

MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF *Rhizomys sinensis troglodytes*

A.M.N.H. Nos.	Greatest Length	Palatal Length	Zygo- matic Width	Mastoid Width	Post- orbital Width	Upper Molars	Incisors ^a	Nasal Suture ^b
18399	—	45.4	—	—	—	15.0	W	—
18401	—	41e	—	—	—	13.1	O	—
18402a	72.2	46.5	—	34.1	9.7	13.9	M	C
18402b	—	47.4	—	—	11.5	14.6	W	C
18402c	70e	45.6	—	30e	12.0	14.1	O	P
18405a	65e	41.6	42e	—	10e	12.5	M	O
18405b	76	47e	—	35.0	11.5	14.0	O	—
18405c	—	—	60e	37.1	9.9	—	—	—
18405d	—	—	—	—	11.0	—	—	—
18406a	74e	47.1	—	32.5	9.3	14.5	O	P
18406b	—	41.7	—	—	—	13.3	O	O
18406c	70e	45.1	—	33.0	11.6	14.2	M	P
18406d	68e	43e	—	32e	9.5	14.0	O	C
18407a	—	49.8	56.5	—	12.0	14.6	O	C
18407b	—	49.7	—	—	9.5	15.5	—	C
18407c	—	47e	—	—	—	15.0	—	—
18407d	—	49.2	—	—	8.2	15.8	O	C
18407e	—	50.0	58.0	—	10.1	14.9	O	P
18407f	—	48.3	58e	—	9.5	14.3	M	—
18408	84.5	52.9	64.0	39.8	10.1	15.7	O	P
18409a	71.9	—	56.0	31.5	9.5	—	O	C
18409b	—	—	—	—	11.4	—	M	P
18409c	—	47.0	—	—	—	13.8	O	—
18409d	72e	45.2	57.0	34.5	11.5	13.8	—	C
18409e	70e	—	51e	—	9.9	—	O	O
18409f	—	46.0	—	—	—	18e	M	—
18409g	—	47.0	—	—	—	15.0	O	—
18409h	—	45.5	—	—	10.9	13.5	—	C
18409i	—	46.0	55.0	—	10.2	13.4	M	C
18409j	—	—	—	—	12.9	13.5	—	—
18409k	—	47e	—	—	9.4	14.2	O	O
18409l	80.0	50.2	60e	36.5	11.4	—	—	—
18409m	—	46.2	—	—	—	13.4	M	C
18409n	76.7	47e	—	35.0	11.5	14.3	M	C
18409o	76.8	48.2	—	36.5	9.6	14.6	O	P
18409p	78.8	50.0	57.0	35.0	9.1	16.1	—	C
18409q	84.2	51.0	—	37.0	9.6	15.3	O	P
18409r	74.9	—	52.0	35.0	9.0	—	M	P
18409s	—	43.0	—	—	—	13.0	O	—
18409t	—	44.5	—	—	—	13.5	O	C
18409u	—	44.7	56.0	—	11.2	13.3	O	C
18409v	—	47e	58.0	32.0	9.6	14.4	O	C
18409w	76.4	48.3	58.0	36.0	9.8	15.0	O	—
18409x	—	46.4	—	—	—	14.5	O	P
18409y	68e	42.6	50.0	31.5	10.5	13.0	O	O
18409z	—	—	—	—	—	—	O	—

^a O, deep orange; M, medium orange; W, white.^b C, closed; P, partially closed; O, open.

TABLE 6—(continued)

A.M.N.H. Nos.	Greatest Length	Palatal Length	Zygo- matic Width	Mastoid Width	Post- orbital Width	Upper Molars	Incisors	Nasal Suture
18409aa	72.6	—	—	—	10.5	—	M	P
18411	—	46.1	—	—	9.2	13.1	O	P
18412a	70e	45.0	—	33.8	9.0	13.3	M	O
18412b	79.1	47.2	—	35.0	9.5	14.4	M	P
18412c	76.5	—	—	—	—	—	O	P
18412d	—	42.1	—	—	—	13.7	O	—
18412e	—	47.2	—	—	—	13.6	M	—
18412f	—	52.5	—	—	9.7	—	O	C
18412g	—	—	—	—	11.2	14.7	—	—
18412h	81.3	51.6	—	—	9.1	16.7	W	P
18413a	—	46.9	—	—	10.9	14.3	O	O
18413b	—	47.4	—	—	10.3	14.1	O	P
18413c	—	47.0	58.0	34.0	10.5	13.5	M	P
18413d	84.0	53.6	—	38.5	9.5	16.3	O	C
18414	78.0	48e	—	33.0	9.5	—	O	P
18415a	79e	46.5	55.0	38.5	8.0	14.3	W	C
18416a	—	49.8	—	—	—	14.7	O	C
18416b	—	52.5	—	—	10.2	15.0	M	O
18416c	—	—	—	—	—	—	O	O
18416d	76.0	—	—	36.0	11.0	—	O	O
18416e	72.4	46e	—	33.0	10.3	14.2	O	P
18416f	76.5	—	—	34.0	10.6	—	O	C
18417a	—	—	—	—	9.7	—	O	P
18417b	—	45e	—	—	—	14.1	O	—
18417c	73.7	46.7	—	33.0	10.3	13.8	M	C
18417d	—	47.0	—	—	11.5	14.5	O	C
18766a	—	47.5	—	—	9.3	15.5e	M	C
18766b	75e	—	—	—	9.4	—	O	—
18769a	78.3	49.5	55	37	9.4	15.1	O	C
18769b	76	49.5	56.4	35.3	11.4	15.0	—	O
18769c	75e	47e	—	35.5	8.5	14.3	—	C
18769d	75.5	47.9	—	35e	11.3	13.3	O	P
18769e	60.5	—	—	28.5	12.2	—	M	P
18769f	—	48.8	—	—	10.2	15.8	O	O
18769g	—	41.5	—	—	—	13.2	M	O
18769h	—	—	—	—	—	14.6	O	—
18770a	74.5	47.3	58.5	35.0	9.3	14.7	O	C
18770b	78.1	47.6	60e	37.4	12.7	14.4	O	—
18770c	79.4	50.8	—	36.9	9.7	15.0	M	O
18770d	—	47.8	58e	—	11.1	14.5	O	O
18770e	79.5	50.9	61	37.3	9.8	15.5	O	C
18770f	74.3	46.8	55.2	33.3	9.4	14.0	O	O
18770g	—	48.5	—	—	9.8	13.9	O	P
18770h	—	50.5	62	—	11.2	15.0	O	—
18770i	—	46.5	58	—	9.1	14.6	M	C
18770j	83.1	52.4	62.9	41.3	9.0	14.9	O	P
18773	—	29.8	—	—	9.9	—	M	—
18774	—	29.2	—	—	—	—	W	—
18777	69	43.3	—	29	9.8	13.9	M	O
18778	75.6	47.7	—	33e	9.7	15.3	O	O

TABLE 7

MEASUREMENTS (IN MILLIMETERS) OF LOWER JAWS OF *Rhizomys sinensis troglodytes*

A.M.N.H. Nos.	Mandible, Length of Symphysis to Condyle	Lower Molars at Alveolus	A.M.N.H. Nos.	Mandible, Length of Symphysis to Condyle	Lower Molars at Alveolus
18400	—	16.9	18587n	59	17.5
18404	—	14.2	18588a	—	16.4
18409a	52.5	16.0	18588b	—	15.3
18409r	52	15.7	18588c	51	15.5
18409aa	—	16.0	18588d	—	16.4
18410a	55a	17.8	18588e	—	16.2
18410b	52	15.7	18588f	—	16.2
18410c	50	15.4	18588h	52	15.5a
18410d	—	17.4	18588i	—	15.7
18410e	55	17.2	18588k	—	15.3
18410f	56	16.8	18588l	—	15.5
18410g	51	17.4	18589a	—	16.8
18410h	50a	16.0	18589c	—	16.8
18410i	50	15.4	18589d	—	16.2
18410j	—	16.3	18590a	46	—
18410k	—	17.1	18590b	45a	14.2
18410l	49	15.0	18590d	—	15.0
18410m	55	16.5	18590e	—	15.3
18410n	—	16.7	18590f	—	8.3
18410o	54	16.0	18590h	—	13.8a
18410p	—	10.7	18591a	50a	15.5
18410q	50a	15.8	18591b	—	17.1
18410r	50	17.2	18591c	—	16.0a
18410s	—	18.5	18591d	52	17.2
18410t	—	9.5	18591e	53	16.0a
18506a	55	15.5	18591g	—	16.6
18506b	—	16.7	18591h	—	15.5a
18506c	49	15.6	18591i	38.5	10.4
18506d	—	16.7	18591j	40.5	10.7
18506e	54	15.8	18591k	53a	16.2a
18506f	50.5	16.7	18591l	—	16.3
18506g	—	17.6	18591m	52	16.9
18506h	—	16.0	18591n	39.5	10.5
18506i	—	16.1	18591o	—	16.6
18585	—	17.8	18591p	—	15.3
18586a	35	8.5	18591q	—	16.5
18586b	14.5	—	18591r	34	10.5
18587a	51	15.6	18591s	—	11.0
18587b	—	15.3	18591t	37	9.9
18587c	39	10.0	18591u	—	10.0
18587d	—	15.5a	18591v	45	15.8
18587e	38.5	9.3	18591w	48	15.7
18587g	52	15.8	18591x	51	16.2
18587h	51	15.4	18591y	57a	18.1
18587i	50a	15.8	18591z	62	17.9
18587j	—	16.3	18592a	51	17.0
18587k	—	16.8	18592b	—	15.8
18587l	54	16.2	18592c	54	17.3
18587m	—	15.9	18592e	50a	14.9

TABLE 7—(continued)

A.M.N.H. Nos.	Mandible, Length of Symphysis to Condyle	Lower Molars at Alveolus	A.M.N.H. Nos.	Mandible, Length of Symphysis to Condyle	Lower Molars at Alveolus
18592f	51	15.5	18594i	—	15.3
18592g	—	16.6	18594j	51	16.2
18592h	—	15.4	18594k	46	15.3
18592j	—	14.9	18594l	—	16.4
18592k	56	16.5	18594m	43	9.0
18592l	49	14.8	18594n	50	15.0
18592m	—	16.1	18594o	—	16.3
18592o	—	15.6	18594p	—	15.5
18592p	45	17.5	18594q	41	10.3
18592q	46.5	15.8	18594r	50	16.8
18592s	54.5	16.9	18594s	56	17.0
18592t	—	15.8	18594t	—	16.5
18592u	—	17.0a	18594u	50.5	16.3
18592v	—	15.7	18594v	—	16.2
18592w	51	15.5	18594w	—	8.9
18592x	49	15.8	18594x	50	15.7
18592y	—	16.7	18594y	45	—
18592z	—	11.4	18594z	—	15.5
18593a	—	10.7	18595a	49	15.1
18593b	53	15.0	18595b	—	15.4
18593c	42	10.0	18595c	48	15.2
18593d	—	16.6	18595d	56	16.3
18593f	—	16.9	18596a	51	16.5
18593g	—	16.4	18596b	55	16.6
18593h	—	15.2	18596c	39.5	11.0
18593i	—	16.1	18596d	45	15.1
18593j	48.5	14.5	18596e	51	16.4
18593k	37.5	10.4	18596g	—	15.6
18593l	—	15.0	18596h	—	15.4
18593m	49	17.0	18596i	—	17.2
18593n	50.5	16.8	18597a	54	15.5
18593o	47	15.9	18597b	56	16.2
18593p	—	10.0	18597c	—	15.7
18593q	40.5	8.8	18597d	—	17.5
18593r	—	11.3	18597e	—	15.4
18593s	46a	14.8	18597f	—	15.4
18593t	49	15.7	18597g	51	15.6
18593u	53	14.8	18598a	58	18.0
18593v	57a	17.6	18598b	52	16.2
18593w	40.5	10.5	18598c	50	16.0
18593x	37	9.9	18598d	—	16.4
18593y	36	10.0	18599	—	14.0
18593z	—	15.6	18600a	45	17.6
18594a	52a	16.3	18600b	—	16.0
18594b	50	15.3	18767a	49.5	16.0
18594c	—	14.8	18767b	56e	17.0
18594d	40.5	10.7	18768a	52	16.5
18594e	—	15.7	18768b	47	15.7
18594f	—	15.5	18768c	53	16.3
18594g	49	15.2	18768d	46	14.8
18594h	—	16.8	18768e	—	15.0

TABLE 7—(continued)

A.M.N.H. Nos.	Mandible, Length of Symphysis to Condyle	Lower Molars at Alveolus
18768f	—	14.3
18768g	57	17.0
18771b	53	17.7
18771c	50	15.5
18771d	54	16e
18771e	53	16.8
18771f	49	15.0
18771g	59	17.8
18771h	41e	—
18771i	57	16.6
18771j	60	17.2
18771k	51.5	15.6
18771l	58.1	15.6
18771m	41	16e
18772a	52	16.0
18772b	52	15.8
18772c	51	15.5
18772d	57	16.9
18772e	—	16e
18772f	48	16.4
18772g	53e	17.7
18772h	53	15.5
18772i	57	16.5
18772j	65	17.3
18772k	57	16.3
18772l	47	14.9
18775	48.5	14.5
18777	49	15.8
18778	54	17.8

jaw of the Yenchingkou *Rhizomys* and the same elements in *Rhizomys sinensis vestitus* leads to the inescapable conclusion that these are closely related subspecies of the same species. There are none of the structural differences, however small, that separate modern species of *Rhizomys* from one another—differences, for instance, on the order of those distinctions in the zygomatic arches, nasals, frontals, premaxillaries, and inter-orbital constriction that separate *Rhizomys sinensis* from *Rhizomys pruinosus*.

The resemblances between *Rhizomys sinensis troglodytes* and *Rhizomys sinensis vestitus* are natural and to be expected. Both forms have inhabited and do inhabit the same region. They are close to each other in geologic time. It may be that the Yenchingkou

Rhizomys is directly ancestral to the modern Szechwan *Rhizomys*. The transition from the former to the latter might be easily effected in skull proportions. On the other hand, it may be that these are separate stocks diverging from a common stem.

Two variable characters in *Rhizomys sinensis troglodytes* should be mentioned in this consideration of the fossil form. First, there seems to be a haphazard variability in the degree of closure of the suture between the two nasal bones. The closing of this suture cannot at the present time be determined. Second, there are all degrees of variability in the color of the upper incisors, which range from a deep orange color through varying shades of orange and yellow, to white. It was stated by Anderson (1879, pp. 321–322) in his detailed study of *Rhizomys* that "The colouring of the teeth is always most brilliant in the male, and more especially in the inferior incisors; while in the female the upper incisors are almost white, and the lower front teeth are richly coloured." The idea of light-colored or white upper incisors in the female seems not to be supported by later authors, nor is it borne out by the material now under consideration, for there is no approximate equal division of the series on the basis of incisor color, as would be expected if it were a sexual character. In fact, very few of the incisors are really white; most of them are preponderantly orange. The color cannot be correlated with size or age characters. So here again is a character which at the present time is considered to be haphazard in its expression. Both of the above characters are indicated in tables 6 and 7.

HYSTRICIDAE

HYSTRIX LINNAEUS

Hystrix LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 56.

GENERIC TYPE: *Hystrix cristata* Linnaeus.

DIAGNOSIS: A large, spiny rodent. Muzzle blunt. Nasal cavity large and nasal bones well developed. Air sinuses in frontals. Upper grinding teeth with one internal and three or four external reentrant folds; lower grinding teeth similar, but with arrangement of folds reversed.

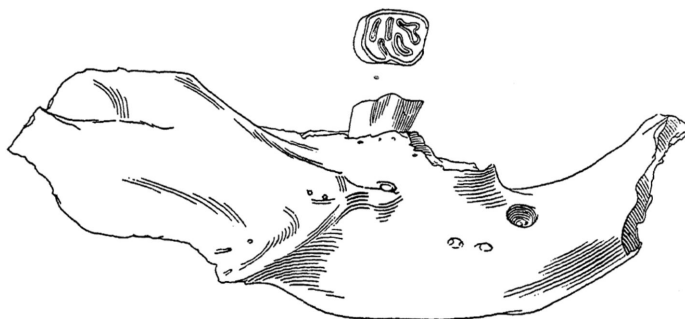


FIG. 14. *Hystrix subcristata* Swinhoe. A.M.N.H. No. 18747, right mandibular ramus with first molar. Lateral view. Natural size.

***Hystrix* cf. *subcristata* Swinhoe**

Hystrix subcristata SWINHOE, 1870, Proc. Zool. Soc. London, p. 638.

SPECIMEN UNDER CONSIDERATION: A.M.N.H. No. 18747, a right mandibular ramus containing the first molar.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DISCUSSION

Hystrix was present in some of the Pleistocene cave or fissure faunas of Asia in great abundance, especially in the regions of southwestern China, Burma, and the Malay area. In fact this porcupine was such a characteristic and abundant part of the Pleistocene faunas in these regions that much of the fossil material is considerably damaged because the bones were gnawed by these rodents before they were fossilized. It is represented at Yenchingkou, however, by only the single fragmentary mandibular ramus listed above.

The specimen from Yenchingkou represents a large porcupine, showing few if any

appreciable differences from the recent form, *Hystrix subcristata*, which ranges over all southern China. The fossil is accordingly referred to the modern species, a procedure similar to that followed by Young in his identification of porcupines from the Pleistocene of Choukoutien, which are approximately contemporaneous in age with the Szechwan fossils.

CARNIVORA

CANIDAE

CUON HODGSON

Cuon HODGSON, 1838, Ann. Nat. Hist., vol. 1, p. 152.

GENERIC TYPE: *Canis primaevus* Hodgson.

DIAGNOSIS: Last lower molar absent and upper molars reduced internally. Muzzle proportionately shorter than in *Canis*.

***Cuon javanicus antiquus* Matthew and Granger**

Cyon antiquus MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 584.

TYPE: A.M.N.H. No. 18389, a pair of

TABLE 8
MEASUREMENTS (IN MILLIMETERS) OF *Hystrix subcristata*

	Yenchingkou A.M.N.H. 18747	Chekiang Wang, 1931	Fukien C.N.H.M. No. 39455
Depth of ramus at P ₄	25.5	28.5	—
M ₁			
L	7.6	7.4	7.5
W	6.7	—	7.3

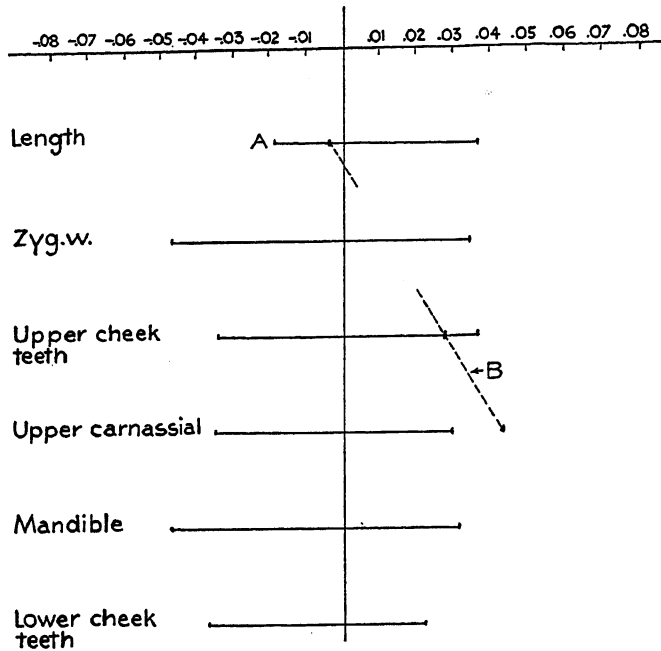


FIG. 15. Ratio diagram of comparative measurements. A. *Cuon javanicus dukhunensis*. B. *Cuon javanicus antiquus*, A.M.N.H. No. 18727.

lower jaws, with right P_3-M_2 and left P_1-M_2 . (This number has been assigned also to some limb bones, probably not representing the same individual as the type jaws.)

REFERRED SPECIMENS: A.M.N.H. Nos. 18391, fragment of maxilla with left M_1 ; 18583, portions of crania, limb bones, and vertebrae; 18727, skull with right and left P_1-M_2 , and left mandibular ramus with M_{1-2} ; 18728, lower jaw (the back of a cranium, including the occipital and basioccipital regions is provisionally associated with the above specimen); 18729, left mandibular ramus with P_2, P_4-M_2 ; 18731, left mandibular ramus, I_1-M_1 ; 18736, left maxilla with P_2, P_4 ; several jaw fragments.

HORIZON AND LOCALITY: Pleistocene; Yen-ching-kou, Szechwan, China.

DIAGNOSIS: "Metaconid distinct upon m_1 and m_2 . Teeth slightly more robust than in our specimens of *C. alpinus*, more decidedly larger and heavier than in *C. javanicus*" (Matthew and Granger, 1923, p. 584).

DISCUSSION

As evident from the list of materials, there are several specimens representing the Orien-

tal hunting dog or dhole in the Yen-ching-kou fauna. Matthew and Granger separated the fossil from the recent forms by its robust teeth and by the presence of the metaconid on the first lower molar. That the teeth of *Cuon antiquus* are large in comparison with those of the recent dholes is evident both from a direct comparison as to general size, as shown in tables 9, 10, and 11 and in plate 6. How much of this difference is due to a relatively larger size for the teeth of the fossil, and how much to the fact that the fossil is throughout more robust than the modern types of this animal is a question difficult to solve satisfactorily. Certainly *C. j. antiquus* is considerably larger than the southern dholes, and this is reflected in the teeth. In this respect it seems to be more nearly comparable to the northern dhole, often separated as a distinct species, *Cuon alpinus*.

The problem is complicated because of the lack of agreement as to the taxonomy of the modern dholes. Some authors recognize several species, notably those comprising the southern type, *Cuon javanicus*, *C. dukhunensis*, and *C. rutilans* (and their synonyms), all of which are considerably smaller

than the northern type, *Cuon alpinus*. Other students, especially Pocock, regard all the modern dholes as being subspecies of a single species, *Cuon javanicus*.

If the former of these two viewpoints is correct, then it is probable that the fossil is a distinct species; if the latter view should hold, then, as Matthew and Granger have said, there might be "some question as to the validity of this species." Thus the Yenchingkou form may be a large subspecies of the species living at the present time.

It is quite certain that the character of a metaconid on the lower carnassial, used by Matthew and Granger for separating the fossil as a distinct form, is valueless. A series of modern dholes, from various parts of the Orient, all show this feature well developed.

Because of the close correspondence in structure between the fossil dhole from Yenchingkou and the existing animal, it has been thought best here to regard the extinct form as a subspecies of *Cuon javanicus*. This subspecific separation of the fossil animal rests mainly on its relatively large size and robustness, especially as regards the dentition, as compared with recent animals from southern Asia. In this respect, *Cuon javanicus antiquus* resembles the northern dhole, *Cuon javanicus alpinus*.

The dholes at the present time are widely spread canids, ranging from India to Fukien and northward into Siberia and Tibet. According to Allen, these animals extended to northeastern China within historic times.

Therefore the presence of *Cuon javanicus antiquus* at Yenchingkou has no particular significance from a distributional standpoint, because even if the dhole is not present in that part of Szechwan at the present time, it was probably there within relatively recent dates. One can say that the Yenchingkou dhole probably represents the direct ancestor of modern types that have lived in or near this region.

URSIDAE

EUARCTOS GRAY

Euarctos J. E. GRAY, 1864, Proc. Zool. Soc. London, p. 692 (as subgenus of *Ursus*).

GENERIC TYPE: *Ursus americanus* Pallas.

DIAGNOSIS: Medium- to large-sized bears in which the muzzle is shortened (as compared with the long muzzle in *Ursus*). As contrasted with *Ursus* the last upper premolar lacks a posterior accessory cusp, while the last upper molar is abruptly narrowed on the outer side behind the metacone. In the first lower molar there is an open space on the inner side between the metaconid and entoconid, while the hypoconid and entoconid are oblique. The last lower premolar lacks an accessory cusp on its inner side.

Euarctos kokeni (Matthew and Granger)

Ursus kokeni MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 580.

TYPE: A.M.N.H. No. 18384, a left mandibular ramus with M_{1-2} .

TABLE 9
MEASUREMENTS (IN MILLIMETERS) OF SKULL OF *Cuon javanicus*

	Length, Pre- maxilla to Condyle	Pre- orbital Length	Post- orbital Length	Palatal Length	Width of Cra- nium	Bulla L×W	Length of Ramus
<i>C. j. dukhunensis</i> , India							
A.M.N.H.(M.) No. 54984	170	68	102	85	65	25.5×17.0	130
<i>C. j. rutilans</i> , Yunnan							
A.M.N.H.(M.) No. 43144	164	60	104	82	65	23.0×16.0	126
<i>C. j. javanicus</i> , "Zoo" specimen							
A.M.N.H.(M.) No. 99636	155	63	94	81	60	24.0×16.0	119
<i>C. j. antiquus</i> , Szechwan							
A.M.N.H. No. 18727	182	67	115	92	69	26.0×18.0	—
A.M.N.H. No. 18728	—	—	—	—	—	26.5×18.0	—

TABLE 10
LENGTH-BY-WIDTH DIMENSIONS (IN MILLIMETERS) OF TEETH OF *Cuon javanicus*

	<i>C. j. dukhanensis</i> , India A.M.N.H.(M.) No. 54984	<i>C. j. rutilans</i> , Yunnan A.M.N.H.(M.) No. 41344	<i>C. j. javanicus</i> , "Zoo" Specimen A.M.N.H.(M.) No. 99636	<i>C. j. antiquus</i> , Szechwan				
				A.M.N.H. No. 18727	A.M.N.H. No. 18389	A.M.N.H. No. 18729	A.M.N.H. No. 18731	A.M.N.H. No. 18736
Upper C	9.2×6.0	9.0×5.2	8.1×5.1	—	—	—	—	—
P ¹	6.0×3.8	5.8×3.6	5.0×3.2	6.5×4.6	—	—	—	—
P ²	9.0×4.6	9.0×5.1	8.0×3.5	9.9×5.3	—	—	—	11.0×5.3
P ³	10.7×5.2	10.8×5.3	10.0×4.2	12.1×6.6	—	—	—	—
P ⁴	19.5×10.0	19.5×9.4	18.8×9.1	22.7×12.0	—	—	—	23.2×11.1
M ¹	11.8×13.8	11.5×14.5	12.0×14.1	13.2×16.9	—	—	11.1×2.8 ^a	—
M ²	4.0×5.9	5.0×7.8	4.3×7.3	5.6×9.1	—	—	—	—
Lower C	9.6×6.6	8.5×6.1	8.1×5.4	—	—	—	10.5×7.8	—
P ₁	5.0×3.5	4.6×3.2	4.6×3.0	—	5.9×4.1	—	5.1×3.8	—
P ₂	8.8×4.6	8.0×4.6	7.9×3.5	—	9.5×4.9	9.0×4.7	9.0×5.3	—
P ₃	9.8×4.8	9.6×4.9	9.3×4.3	—	10.6×5.5	—	10.2×5.7	—
P ₄	12.3×6.1	12.2×6.1	11.7×5.0	—	15.9×6.8	13.5×6.6	13.2×6.8	—
M ₁	20.1×7.9	20.6×9.5	19.7×7.8	22.1×8.5	25.4×9.0	22.5×8.8	23.3×9.5	—
M ₂	6.7×5.5	6.5×5.8	6.4×5.4	7.6×6.3	8.5×7.1	8.3×7.0	—	—
Talonid, M ₁	5.3×6.4	5.2×6.9	4.9×6.6	5.6×7.6	7.2×8.0	6.2×7.4	—	—

^a A.M.N.H. No. 18391.

REFERRED SPECIMEN: A.M.N.H. No. 18735, an associated skull and mandible. The skull lacks the top of the cranium, the zygomatic arches, the median incisors, and anterior premolar teeth; the mandible lacks the tips of the coronoid processes, all but one of the incisors, the premolars in front of P₄ on both sides, and the right M₃. The specimen is somewhat crushed.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: "Jaw very short and deep as in the sun-bear *U. malayanus*, but size large, comparable with *U. arctos*; m₁ narrow and long, lacking the metastylid cusp of *U. malayanus*; m₂ rather short and wide, wider posterior than anteriorly" (Matthew and Granger, 1923, p. 580).

DISCUSSION

Matthew and Granger, having before them only the type specimen, said nothing be-

TABLE 11
RATIOS AND INDICES OF *Cuon*

	A.M.N.H.(M.) No. 54984	A.M.N.H.(M.) No. 41344	A.M.N.H.(M.) No. 99636	A.M.N.H. No. 18727
Length palate/length skull	50	50	52	51
Length P ⁴ /length palate	23	24	23	25
Length M ¹ /length P ⁴	60	59	64	58
Length M ² /length P ⁴	21	26	23	25
Length M ₁ /length mandible	15	16	17	—
Length M ₂ /length M ₁	33	32	33	34

yond the statements in their original diagnosis quoted above. Subsequently, Granger discovered a good skull and mandible at Yenchingkou, which add materially to our knowledge of the species and are discussed below.

Matthew and Granger compared the type mandible of this species with that of the sun bear, *Helarctos malayanus*, and of the Eurasian brown bear, *Ursus arctos*. A careful examination of the new skull and jaw leads, however, to the inevitable conclusion that this fossil form from Yenchingkou is related to the Asiatic black bears belonging to the

genus *Euarctos*. It is large, for which reason it might be thought to have affinities with the *Ursus* group, but anatomically, particularly in those characters of the skull and dentition utilized by Merriam in 1896 to distinguish the bears of the genus *Euarctos*, this Szechwan fossil is in every particular referable to the latter genus (see Allen, 1938, p. 331).

It is quite large, much larger than the American black bears, typified by *Euarctos americanus*, and considerably larger than the Asiatic black bear, *Euarctos thibetanus* (= *Euarctos torquatus* of some authors). In all its structural features *Euarctos kokeni* is

TABLE 12
MEASUREMENTS (IN MILLIMETERS) OF SKULL AND TEETH OF *Euarctos*

	<i>E. kokeni</i> , Type A.M.N.H. No. 18384	<i>E. kokeni</i> A.M.N.H. No. 18735	<i>E. thibetanus</i> A.M.N.H.(C.A.) No. 1981
Length			
Premaxilla to condyle	—	300.0	273.0
Palatal	—	160.0	141.0
Preorbital	—	94.0	90.0
Postorbital	—	206.0	183.0
Width			
Zygomatic	—	200.0	159.0
Occipital	—	170.0	134.0
Postorbital constriction	—	72.0	60.5
Brain case	—	141.0	91.5
Palate at M ₁	—	42.0	40.0
Height, occiput	—	85.0	66.5
L×W			
I ³	—	8.7×9.9	8.5×8.3
Upper C	—	22.3×14.5	20.0×13.0
P ⁴	—	14.5×9.8	13.0×8.9
M ¹	—	20.3×15.8	18.2×13.5
M ²	—	30.7×16.5	27.4×13.9
Length			
P ₁₋₄	—	30.0	40.0
M ₁₋₂	—	50.0	44.4
Length, incisors to condyle	—	207.0	188.0
Depth at M ₁	51.0	50.0	39.0
L×W			
I ₃	—	7.4×8.8	7.4×8.1
Lower C	—	20.0×14.7	19.6×12.7
P ₄	—	11.3×7.2	11.2×6.0
M ₁	22.6×9.2	21.7×9.4	20.0×8.4
M ₂	21.2×13.7	20.7×13.1	20.2×10.9
M ₃	—	16.9×12.3	17.0×11.9
Length			
P ₁₋₄	—	36.5	40.5
M ₁₋₃	—	60.0	57.0

closely comparable to *Euarctos thibetanus*, differing from this latter form mainly in having a more robust build.

As a result of the large size of *Euarctos kokeni*, the skull is broad and heavy, especially in the occiput, and it would seem that the sagittal crest was relatively heavier than in the modern Asiatic black bear.

As is typical of *Euarctos*, the Yenchingkou bear is characterized by the sudden exterior constriction of the last upper molar behind the metacone, the lack of any cusps between the metaconid and the entoconid in the lower carnassial, and the obliquity of the hypoconid and entoconid in this latter tooth.

Incidentally, the metastylid cusp, the lack of which Matthew and Granger supposed to be distinctive for *Euarctos kokeni*, actually is present (though very small) in this species, as shown by the supplementary material. The first three premolars above and below in the Asiatic black bear are very small, and such must have been the case to an even greater degree in the fossil form, in which small alveoli for these teeth are visible. It is interesting to see that in the larger extinct species the space for the first three premolars is not only relatively but also actually shorter than the same space in the recent form. Throughout the dentition, the teeth of *Euarctos kokeni* are broader and heavier than comparable teeth in *E. thibetanus*, because of their greater size in the fossil species. As regards the second lower molar, however, the difference is greater than is to be accounted for merely by the natural growth increments that might be expected as a result of a general size increase. In this one tooth, therefore, there seems to have been a differential increase in transverse growth in the extinct species, making the molar broad in comparison not only with its own length but also with the width of the carnassial preceding it—a condition not seen in the recent species.

All in all, the resemblances between the two forms are much more striking than the differences.

PROCYONIDAE

AILUROPODA MILNE-EDWARDS

Ailuropoda A. MILNE-EDWARDS, 1870, Ann. Sci. Nat., Paris, zool., ser. 5, vol. 13, art. 10, p. 1.

GENERIC TYPE: *Ursus melanoleucus* David.

DIAGNOSIS: A very large procyonid with strong jaws and zygomatic arches, canines reduced in size, cheek teeth enlarged and adapted to a herbivorous diet, carnassials with shear secondarily suppressed, molars with broad occlusal surfaces, complicated by numerous small conelets and wrinkles. Skeleton heavy and tail short.

Ailuropoda melanoleuca fovealis (Matthew and Granger)

Aeluropus fovealis MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 579.

TYPE: A.M.N.H. No. 18385, right mandibular ramus with P_4 - M_3 ; also a left M_3 of the same individual.

REFERRED SPECIMENS: A.M.N.H. Nos. 18386, right P_4 ; 18387, fragments of right and left mandibular rami with right M_1 and the anterior portion of left M_1 ; 18388, left mandibular ramus with M_{1-2} ; 21770, skull and mandible, the skull lacking the front of the muzzle and the zygomatic arches, but with right P_4 - M^2 and left C, P^2 - M^2 , the mandible lacking a portion of the symphyseal region and the left condyle, but with the roots of the incisors, a broken right C, right P_2 - M_3 and left C, P_3 - M_3 ; 21771, fragments of left and right mandibular rami with M_{2-3} on both sides; 21772, fragments of left and right mandibular rami with portion of right M_1 and left M_{2-3} ; 21773, mandible with right P_3 - M_3 ; 21774, portion of right mandibular ramus with M_{1-3} ; 21775, portion of left mandibular ramus with P_{3-4} and broken P_2 and M_1 ; 21776, portion of left mandibular ramus with M_{2-3} ; 21777, right M^1 , M^2 ; 21778, left M_3 ; also distal ends of two right and three left humeri; 39216, right M_3 .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: "The teeth resemble those of *A.E. melanoleucus* as figured by Lankester, 1901, except in the following particulars: the protocone of p_4 is distinctly higher than the anterior and posterior cusps; m_1 retains more of the normal carnassial construction, the anterior end being less quadrate, protoconid larger, paraconid more advanced and the whole tooth is relatively

larger; m_2 and m_3 are broader, though not longer . . . the differences noted above [may be] individual rather than specific. However, as it seems unlikely that a species of the Carnivora would persist unchanged from the Pliocene to the present day, it appears better to regard the species provisionally as distinct" (Matthew and Granger, 1923, p. 579).

DISCUSSION

When Matthew and Granger made their original study of the giant panda from the Szechwan fissures, they had before them some fragmentary lower jaws, a portion of a premaxilla, and some separate teeth. It would seem that they had very little material of the modern panda for comparative purposes, since according to their description many of the resemblances and differences were based, at least in part, on comparisons with published figures of the recent panda. After the publication of the first Szechwan paper a considerable amount of additional material of the fossil *Ailuropoda* was obtained, as listed here under referred specimens, while a series of skulls and jaws of the modern panda is now available for comparative purposes.

Thus with the increased opportunity for a more complete comparison of the recent and fossil pandas than was possible when the first studies of the Szechwan collection were made, it would seem that the differences between the fossil and recent forms are not so great as was formerly supposed. The characters cited by the original authors as distinctive of *Ailuropoda melanoleuca fovealis* are examined in sequence.

Matthew and Granger thought that the "protocone" of the last lower premolar in *A. melanoleuca fovealis* was relatively higher in comparison to the anterior and posterior cusps of the same tooth than in the recent panda, but a careful comparison of all the fossil and recent material now at hand shows that this supposed difference is not valid.

Those authors also considered the lower carnassial in the fossil as being somewhat more like the typical carnivore carnassial than is the case in the modern animal. This supposition was based on the supposedly less quadrate anterior end of the carnassial in the fossil, the larger protoconid, and the more advanced paraconid. Here again a

comparison of the truly adequate series made available by the second and third collecting seasons at Yenchingkou with a series of modern pandas shows that the characters cited as distinctive are not valid.

Again, the relatively larger size of the lower carnassial in the fossil type cited by Matthew and Granger seemingly is not a valid character, and the same objection can be made with regard to the supposed relatively larger posterior molars, as described by them.

From this it becomes apparent that of the various characters listed by Matthew and Granger as being distinctive for the fossil as compared with the modern panda, none will hold when an attempt is made to distinguish the two forms from each other. Nevertheless, on the basis of skulls, jaws, and dentitions, it is possible to separate the fossil and recent forms, as follows:

1. The fossil is undoubtedly larger and heavier throughout than the modern panda. Because of this a number of structural differences can be seen between the two supposed species.

2. Thus the postorbital constriction of the cranium is less marked in the fossil than in the recent panda.

3. Also the sagittal crest is heavier and relatively lower in the fossil than in the recent species. The crest is more distinct from the parietal roof in the recent species than in the fossil.

4. Similarly, the postglenoid processes of the fossil form are heavier than in the recent species, and they do not curve around under the glenoid so markedly in the extinct form as they do in the modern panda.

5. The occiput of the fossil type is broader, as are the occipital condyles, as might be expected.

6. Again, as one would expect, the mandible of the fossil is more robust than that of the recent form.

7. Finally, the teeth of the fossil form are considerably more robust than in the modern species.

From the foregoing it becomes evident that only with regard to a few particulars can the fossil panda be separated from the recent animal. The fossil form is uniformly larger and more robust than the modern

TABLE 13
MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF *Ailuropoda melanoleuca*

	<i>A. m. fovealis</i>	<i>A. m. melanoleuca</i>			
	A.M.N.H. No. 21770	A.M.N.H.(M.) No. 89029 ♀	A.M.N.H.(M.) No. 110451 ♀	A.M.N.H.(M.) No. 110454 ♀	A.M.N.H.(M.) No. 87242 ♂
Length					
Premaxilla-condyle	260a	255.5	246.0	255.0	259.0
P ² -condyle	230a	226.0	217.0	226.0	225.0
Width					
Parietal	112a	96.0	99.0	97.0	99.0
Postorbital	54a	45.0	37.5	41.0	47.0
Zygomatic	220a	207.0	202.0	193.5	215.0
Occipital	153a	152.0	143.0	142.0	163.0
Height					
Occipital	86a	87.0	86.0	78.0	87.0
Postglenoid-sagittal crest	145a	135.0	135.0	134.0	144.0

TABLE 14
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Ailuropoda melanoleuca*

	A.M.N.H. No. 21770	A.M.N.H. No. 18386	Kwangsi Pei, 1935	Yunnan Bien and Chia, 1938	Recent U.S.N.M. ^a	Recent A.M.N.H.(M.) ^b
C						
L	18.3	—	—	—	14.8– 20.4	15.7–18.1
W	14.4	—	—	—	10.3– 13.9	10.7–13.1
P ¹						
L	—	—	—	—	3.3– 4.4	3.2– 4.5
W	—	—	—	—	2.5– 4.3	3.4– 4.6
P ²						
L	14.5	—	—	—	12.1– 14.2	13.1–13.8
W	8.5	—	—	—	6.1– 7.4	6.5– 7.4
P ³						
L	22.0	—	—	22.1–22.8	18.2– 21.0	19.4–20.2
W	13.0	—	—	12.4–11.3	10.8– 12.8	11.7–12.4
P ⁴						
L	27.7	28.5 ^c	30.0	26.2	22.6– 26.7	24.3–25.8
W	19.2	20.8 ^c	20.0	18.0	16.8– 20.1	17.2–19.1
M ¹						
L	27.4	28.6	26.0	26.0–27.0	22.4– 26.2	22.8–24.5
W	30.0	31.5	28.0	28.4–30.0	25.1– 29.6	26.3–27.8
M ²						
L	35.8	37.7	34.2–40.5	31.0–34.0	30.4– 36.5	32.1–35.8
W	28.1	30.5	24.0–30.4	25.3–27.3	24.0– 28.2	24.5–26.2
P ² –M ² , L	108.2	—	—	—	93.5–106.8	—

^a Fifteen specimens.

^b Four specimens.

^c A.M.N.H. No. 21777.

TABLE 15
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Ailuropoda melanoleuca*

	A.M.N.H. No. 21770	A.M.N.H. No. 18385	A.M.N.H. No. 18387	A.M.N.H. No. 18388	A.M.N.H. No. 21772	A.M.N.H. No. 21773	A.M.N.H. No. 21774	A.M.N.H. No. 21775	Kwangsi, Pei, 1935	Yunnan, Bien and Chia, 1938	Recent	U.S.N.M. ^a	Recent	A.M.N.H. (M) ^b
C														
L	20.9	—	—	—	—	—	—	—	—	—	15.9–	20.6	14.7–18.5	
W	15.7	—	—	—	—	—	—	—	—	—	10.7–	14.4	10.2–15.3	
P ₂														
L	12.6	—	—	—	—	—	—	—	—	—	9.3–	12.4	11.0–11.9	
W	8.0	—	—	—	—	—	—	—	—	—	5.7–	7.1	6.0–7.0	
P ₃														
L	18.3	—	—	—	—	18.4	—	17.5	19.0	16.8	14.8–	18.3	16.0–17.3	
W	10.8	—	—	—	—	10.8	—	10.0	10.3	8.6	8.1–	10.2	9.1–10.0	
P ₄														
L	24.3	22.5	—	—	—	25.8	—	24.1	25.0	23.9	20.5–	23.7	21.9–24.2	
W	14.4	12.9	—	—	—	14.6	—	14.4	12.6	12.5	11.0–	13.9	11.9–13.1	
M ₁														
L	33.9	32.0	35.0	—	—	36.8	34.5	—	37.0	—	28.4–	32.6	30.5–31.0	
W	20.7	19.7	18.6	22.3	—	23.8	23.0	—	22.5	—	16.7–	20.8	18.3–19.7	
M ₂														
L	27.2	24.4	30.0 ^c	28.3	28.7	28.8	28.6	28.2 ^d	27.5–28.0	—	22.9–	26.5	24.2–26.5	
W	22.9	20.0	24.8 ^c	25.4	23.1	25.2	24.3	23.8 ^d	22.0–23.2	—	18.0–	23.3	19.3–22.0	
M ₃														
L	20.3	16.8	23.6 ^c	21.8 ^c	18.5	19.9	20.0	17.5 ^d	19.0	17.0–20.0	16.5–	21.3	16.8–18.9	
W	21.3	18.7	23.9 ^c	22.2 ^c	22.3	24.5	22.8	22.1 ^d	21.4	19.8–20.8	17.7–	22.0	18.4–20.0	
P ₅ –M ₃ , L	123.5	—	—	—	—	128.7	—	—	—	—	102.3–112.8	—	—	
M ₁ –M ₃ , L	80.0	71.8	—	—	—	86.3	83.5	—	—	—	67.7–	78.8	71.5–74.1	

^a Fifteen specimens.

^b Four specimens.

^c A.M.N.H. No. 21771.

^d A.M.N.H. No. 21776.

^e A.M.N.H. No. 21778.

panda, a difference that is virtually harmonic throughout the morphological structure, without any marked differences due to changes in proportion. Moreover, the fossil shows a few minor differences from the modern panda, notably in the heavier construction of the sagittal crest, the lesser constriction of the postorbital portion of the cranium, and a slightly different construction of the postglenoid region. For these reasons, and particularly because of the size differences, the panda from Szechwan is hereby considered a subspecies of the mod-

ern form, *Ailuropoda melanoleuca fovealis*.

Pei (1935) and Bien and Chia (1938) have recorded fossil *Ailuropoda* teeth from Kwangsi and Yunnan, respectively, and the measurements are entered in our table 15. It will be seen that some of the teeth recorded are larger, others smaller, than those in our Yen-ching-kou series. The range of variation of measurements of the recent giant panda is based on a series of 15 skulls in the Graham collection of the United States National Museum, most, if not all, obtained at Wen Chuan Hsien, Szechwan.

TABLE 16
MEASUREMENTS (IN MILLIMETERS) OF *Charronia flavigula*

	Length	Palatal Length	Zygomatic Width	Mastoid Width	Width Across Molars	Length C-M ¹
<i>C. f. tyrannus</i>						
A.M.N.H. Nos.						
18717	108.0	49.7	66.4	47.0	35.2	36.0
18723	—	—	—	40.6	—	—
<i>C. f. flavigula</i>						
A.M.N.H.(M.) Nos.						
38331 ♂	100.7	47.5	56.0	45.0	34.0	34.0
43147 ♀	91.5	42.7	48.5	43.0	30.3	30.8
43148 ♂	99.0	48.0	55.5	44.5	31.8	32.8
43149 ♀	94.2	44.4	55.0	43.2	32.0	32.2
57046 ♂	99.5	45.5	58.7	46.0	36.8	32.4
59317 ♀	89.2	40.6	52.2	39.7	29.0	29.1
84445 ♀	92.4	42.5	53.5	42.0	29.3	30.2
84447 ♀	—	50.4	65.0	48.2	34.0	34.8
84894 ♀?	96.0	45.0	52.7	41.5	30.0	32.2
87391 ♂	99.0	45.7	59.2	42.2	32.2	33.2
110472 ♀	96.0	42.5	57.0	43.8	30.6	30.5

MUSTELIDAE

CHARRONIA GRAY

Charronia J. E. GRAY, 1865, Proc. Zool. Soc. London, p. 108.

GENERIC TYPE: *Mustela flavigula* Boddaert.

DIAGNOSIS: A large marten distinguished from *Martes* by the structure of the baculum, which is abruptly turned upward distally and has the tip divided into four short processes (Pocock); the upper lip does not have the vertical groove in the middle as in *Martes*; P⁴ trenchant, M¹ about one and one-half times wider than long.

Charronia flavigula tyrannus, new subspecies

TYPE: A.M.N.H. No. 18717, skull, complete except for the absence of the left I¹, the lateral incisors, and the canines.

PARATYPES: A.M.N.H. No. 18723, a cranium, with that portion of the skull anterior to the postorbital processes missing; A.M.N.H. No. 18724, a left mandibular ramus with P₄, M₁.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Like the modern yellow-throated marten, *Charronia flavigula flavigula*, but larger.

DISCUSSION

In a qualitative way there is very little to distinguish this Szechwan form from its modern counterpart, the yellow-throated marten of China. It is a large marten, as is the modern form, characterized by its short face and by the rounded and expanded brain case. The front of the orbit is above the anterior edge of the upper carnassial, and beneath the orbital rim is a large infraorbital foramen. There is virtually no postorbital constriction, the olfactory portion of the brain case being very broad, as in the modern animal, while low temporal ridges run back from the postorbital processes to the lambdoidal crest, paralleling each other but never meeting on the top of the broad, rounded cranium. The occiput is low and broad. The auditory bullae are large and inflated, being perhaps slightly more prominent than the same structures usually are in the modern oriental marten of this type. Otherwise the basicranium of the extinct Szechwan animal is quite similar to the same region in *Charronia flavigula flavigula*.

The teeth are heavy and robust, as might be expected in so large a *Charronia*. Otherwise there is nothing to distinguish them from the teeth of the modern animal. As in the

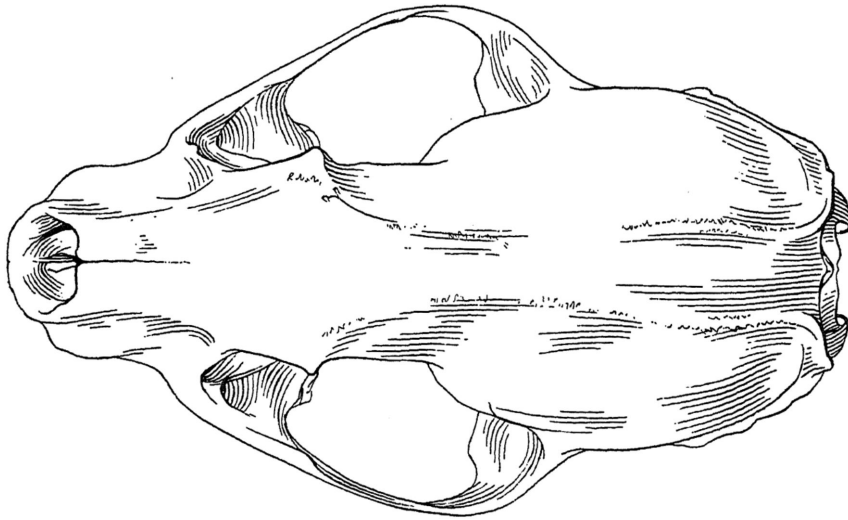


FIG. 16. *Charronia flavigula tyrannus*, new subspecies. Type, A.M.N.H. No. 18717. Skull. Dorsal view. Natural size.

modern form the dental formula is limited by the loss of the last two upper molars and the last lower molar.

Perhaps the relationship of the extinct marten from Szechwan, *Charronia flavigula tyrannus*, to its recent counterpart, *Charronia flavigula flavigula*, can best be shown by the method of the ratio diagram, as described above. In this case *Charronia flavigula flavigula* was used as a standard for comparison, the skulls listed and measured in Allen's monograph of the recent mammals of China and Mongolia (Allen, 1938, p. 365) being compared with the specimens from Yenchingkou.

From the ratio diagram (fig. 19) it is readily seen that in all measurements except that of the zygomatic width, the extinct form, as known from the type skull, comes within the range of size variation of the recent yellow-throated marten living in this region of China. But it is considerably larger than the average for the modern form.

It might be argued that since the measurements of the extinct animal come for the most part within the range of measurements for the modern subspecies from western China, we are dealing here only with a large variant of the modern type rather than with a distinct subspecies, and this may be true. However, it is to be noted that only by the presence in the series of a very abnormally

large modern animal is this possible; it is shown by the diagram that a typically large *Charronia flavigula flavigula* is noticeably smaller than the fossil. In the light of our

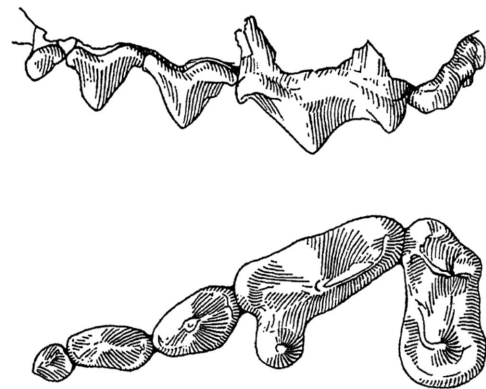


FIG. 17. *Charronia flavigula tyrannus*, new subspecies. Type, A.M.N.H. No. 18717, left P1-M2. Lateral and crown views. Twice natural size.

knowledge of the general size trend of the Yenchingkou mammals compared to their modern counterparts, it therefore seems expedient at this time to consider the extinct form as representative of a truly distinct subspecies of large size.

ARCTONYX CUVIER

Arctonyx F. CUVIER, 1825, Histoire naturelle des mammifères, vol. 3, pt. 51, pl. and 2 pp. text.

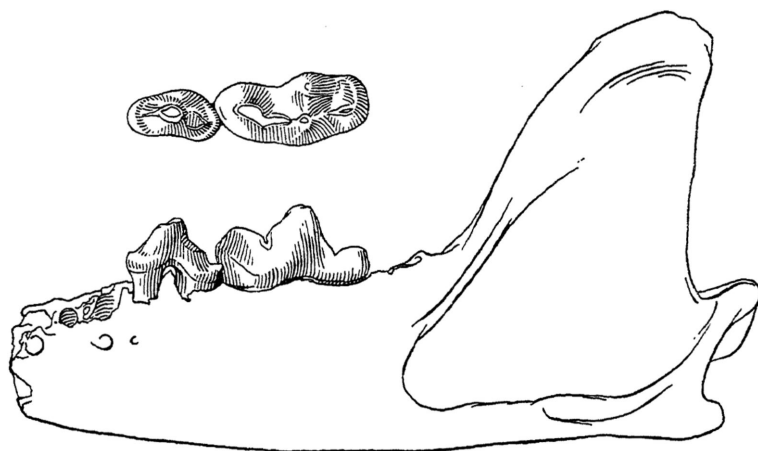


FIG. 18. *Charronia flavigula tyrannus*, new subspecies. A.M.N.H. No. 18724, left mandibular ramus with P_4 and M_1 , lateral view. Crown view of P_4 and M_1 . Twice natural size.

GENERIC TYPE: *Arctonyx collaris* F. Cuvier.

DIAGNOSIS: A badger distinguished in the skull by the very large infraorbital foramen, small bullae, and particularly by the backward extension of the palate to a point opposite

the glenoid fossae. Dentition 3-1-4-3, with the anterior premolars very small and in some cases absent. Upper molar broad, with accessory lingual ridge; lower carnassial elongated and narrow, with a large talonid.

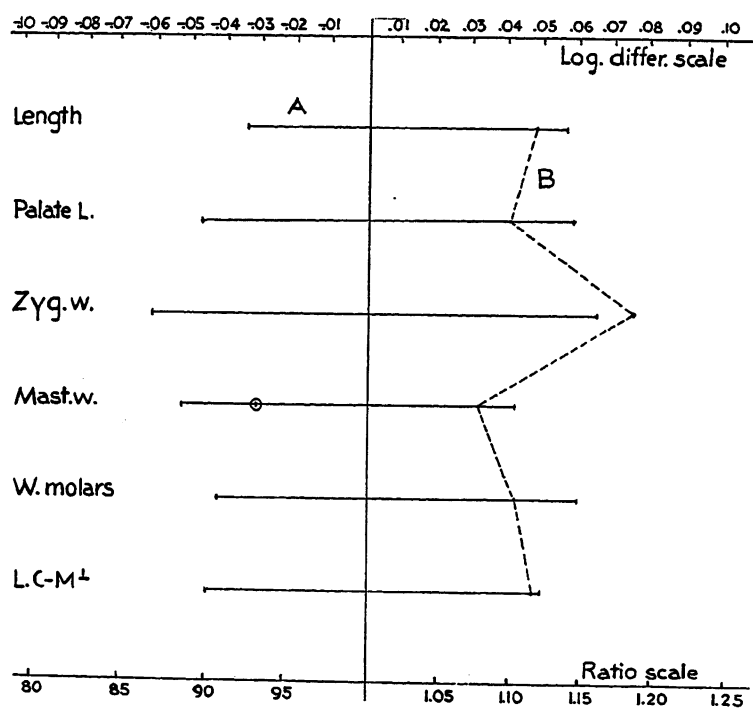


FIG. 19. Ratio diagram of comparative measurements. A. *Charronia flavigula flavigula*. B. *Charronia flavigula tyrannus*, A.M.N.H. No. 18717.

***Arctonyx collaris rostratus* Matthew and Granger**

Arctonyx rostratus MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 580-583.

TYPE: A.M.N.H. No. 18393, a skull, lacking the zygomatic arches and all the teeth except the crowns of left I^3 , P^4 , and M^1 .

PARATYPES: A.M.N.H. Nos. 18381, a left mandibular ramus and symphysis, with P_4 , M_1 ; 18382, a right mandibular ramus with M_1 ; 18394, a skull lacking most of the muzzle in front of the orbits, the zygomatic arches, and all the teeth except for fragments of the molars on either side, but with the condyles and coronoids of the two rami attached to the skull.

REFERRED SPECIMENS: A.M.N.H. Nos. 18718, a very fine associated skull and mandible of an old individual of large size, lacking the occiput, the left zygomatic arch, the upper incisors, and certain anterior premolars and the lower incisors; 18722, postorbital portion of skull, lacking zygomatic arches, of a very large individual; 21781, an extraordinarily fine skull and mandible, complete except for the upper canines, which dropped out before fossilization took place.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: "Length of skull, premaxillae to condyles, 148 mm.; sagittal crest narrow, distinct; p_1^1 absent, p_2^2 larger than in *A. col-*

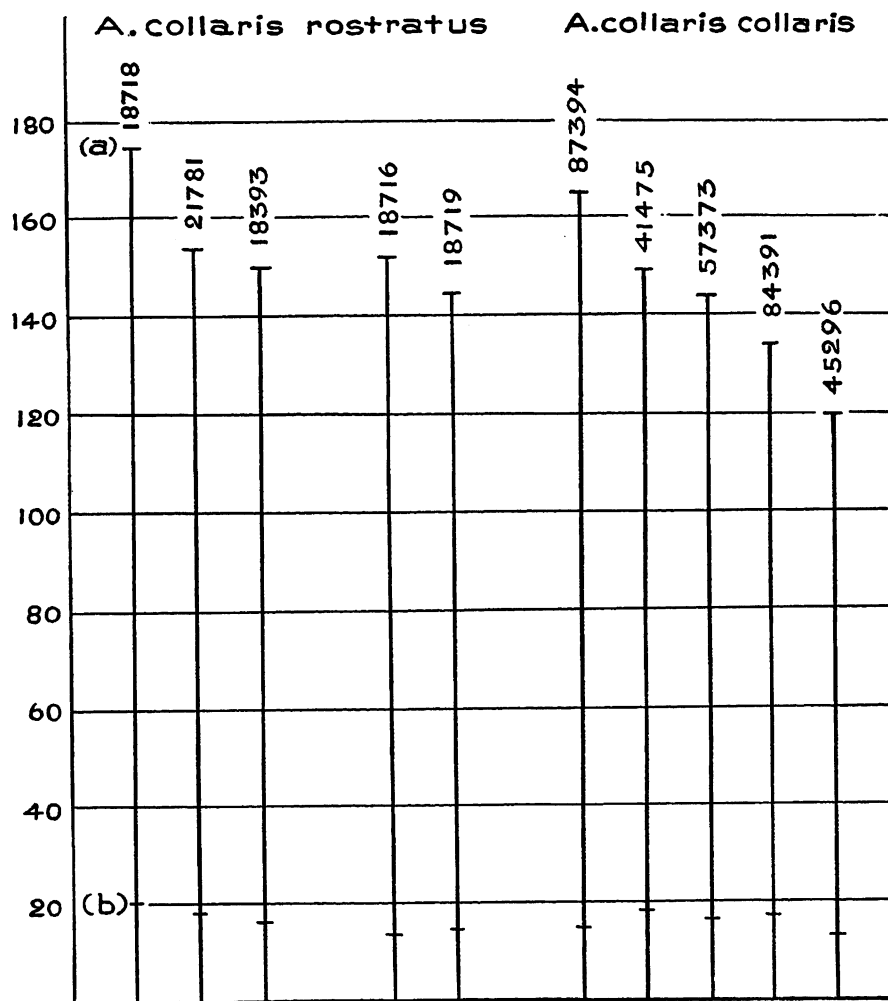


FIG. 20. Diagram showing lengths of skull (a) and M^1 (b) in specimens of *Arctonyx collaris rostratus* and *Arctonyx collaris collaris*.

laris and more clearly two-rooted, the diastema behind p^2 greater than length of p^3 ; p^4 larger with inner cusp better developed and more antero-internal; m^1 larger, broader and more quadrate in form; auditory meatus and posttympanic process broad, massive and flattened, occiput broader at the base. P_3 and p_4 are more robust than in *A. collaris* and there is no diastema between them; m_1 and m_2 are considerably larger and more robust, with the cusps more conical in form" (Matthew and Granger, 1923, pp. 580-583).

DISCUSSION

The hog-nosed badger, *Arctonyx*, is represented in the cave fauna from Yenching-kou by a series of skulls and jaws, which includes several extraordinarily fine specimens. Attention should be called particularly to A.M.N.H. Nos. 18718 and 21781, associated skulls and jaws in an unusually complete state of preservation.

Matthew and Granger distinguished the Yenching-kou specimens as belonging to a distinct species, *Arctonyx rostratus*. Unfortunately, as in the case of some of the other Szechwan fossil forms, these authors lacked the fine material that now characterizes the collection. Consequently, most of the supposed differences delineated between *Arctonyx rostratus* and the recent species, *Arctonyx collaris*, will not hold on the basis of a comparison of an adequate series of well-preserved fossils and a similar series of the modern species.

The one difference most noticeable between the fossil and recent specimens is size. Thus the fossil skulls and jaws seem to be generally, although not invariably, larger than recent specimens. This is especially noticeable in the case of the large Yenching-kou individuals, A.M.N.H. Nos. 18718 and 18722. Yet as regards size, the supposed fossil species overlaps the range of variability shown by the modern type, as may be seen from tables 17, 18, and 19 and from the graphs (figs. 20, 21) showing skull lengths and dimensions of the first molars. Incidentally, there is a surprisingly large range of variation in the modern species, both as to size and as to form. For instance, the smallest skull in the series of recent specimens at hand is some 30 per cent smaller than the largest skull

attributed to the same species. Again, there is a very great range of variation in skull and tooth proportions in the recent species. Some of the short skulls are very broad across the zygomatic arches, while some of the longer skulls are relatively narrow. In some of the small skulls the teeth are large, while in some of the large skulls the teeth are small. With differences such as these in a single modern species, it is not to be wondered at that the delineation between the fossil from Yenching-kou and the recent form is difficult and rather tenuous.

Therefore, except for a certain, and at best a rather dubious, distinction based on size, the differences between the fossil and recent forms are small. In the fossil the first upper premolar is consistently absent, while the diastema behind the second upper premolar is usually longer than in the recent species. Otherwise the dissimilarities are not so marked as Matthew and Granger supposed them to be. For instance, the prominent sagittal crest so characteristic of the Yenching-kou specimens is an age character, typical of fully adult individuals, and it can be seen in old individuals of the modern form, as pointed out by Allen (1938). Most of the other supposed differences are likewise characters associated with size and age. This is particularly true in the dentition, notably the supposedly larger cheek teeth in the fossil. Also the absence of the first lower premolar, used by Matthew and Granger as a character distinctive of *Arctonyx rostratus*, will not hold on the basis of an adequate series of fossils. This tooth is variable, in the fossil being sometimes present and sometimes absent, although its counterpart in the maxilla seems to be always absent. In the recent form both the upper and lower first premolars are variable, being in some cases present and in others absent.

Throughout most of its anatomical features, the skull of *Arctonyx rostratus* is very similar to that of *Arctonyx collaris*, showing those characters particularly diagnostic for this oriental badger. Thus the infraorbital foramen is very large in the fossil, as it is in the recent form, while the auditory bulla is rather flat. The palate is prolonged backward, a very distinctive feature for the genus, so that its posterior border is opposite or

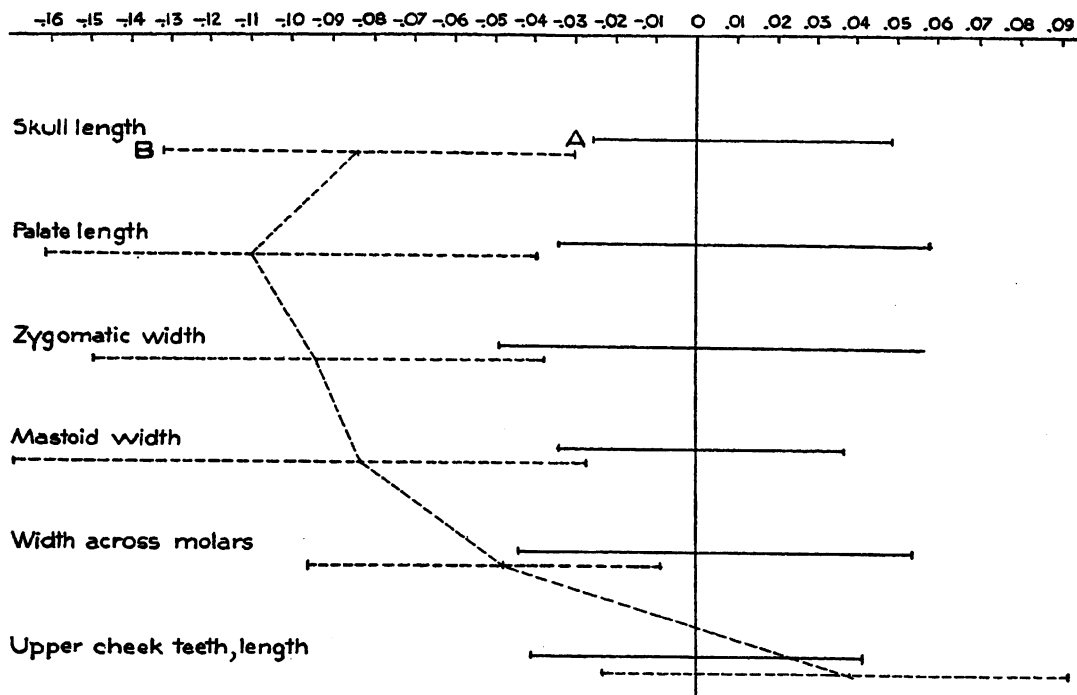


FIG. 21. Ratio diagram of comparative measurements. A. Four specimens of *Arctonyx collaris rostratus*. B. Thirteen specimens of *Arctonyx collaris collaris*. Dotted line connects means in B.

behind the glenoid fossa and is formed by the pterygoids. The profile of the muzzle is sloping from the supraorbital region to the tips of the nasals.

Since the specimens representative of the extinct form are seen to grade into those typical of the modern species, it seems best to regard *Arctonyx rostratus* as a subspecies of *A. collaris*. In doing this we confine the name *A. collaris rostratus* to the larger, well-fossilized specimens from Yenchingkou. Certain specimens from Yenchingkou comparable to the larger specimens of the recent form and showing little if any fossilization are here considered as being subspecifically the same as the modern type.

Arctonyx collaris collaris Cuvier

Arctonyx collaris F. CUVIER, 1825, Histoire naturelle des mammifères, vol. 3, pt. 51, pl. and 2 pp. text.

TYPE: This species was based on a colored drawing sent to F. Cuvier by M. Alfred Duvaucel.

REFERRED SPECIMENS: A.M.N.H. Nos. 18716, associated skull and mandible, the

skull lacking the anterior portions of the maxillaries, the right zygomatic arch, the right condyle, the canines, left I^{2-3} and right P^2 , the mandible lacking the left I_3 , P_{1-3} , M_2 , and the anterior portion of the right M_1 ; 18719, fragments of a skull and mandible, partially preserved on the right side, with P^2 , P^4 , M^1 present, while the left maxilla is present with P^1 - M^1 . Left mandibular ramus with P_4 , M_1 , right mandibular ramus with M_{1-2} .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China. Recent; throughout much of China and India.

DIAGNOSIS: See the diagnosis for the genus, above. In addition, the recent animal is distinguished by certain details in the coloration of the pelage, as described by various authors.

DISCUSSION

The two specimens listed above from Yenchingkou are hereby referred to *Arctonyx collaris collaris* rather than to *A. collaris rostratus* because of their close resemblance to the modern form and particularly because of the comparatively fresh condition of the

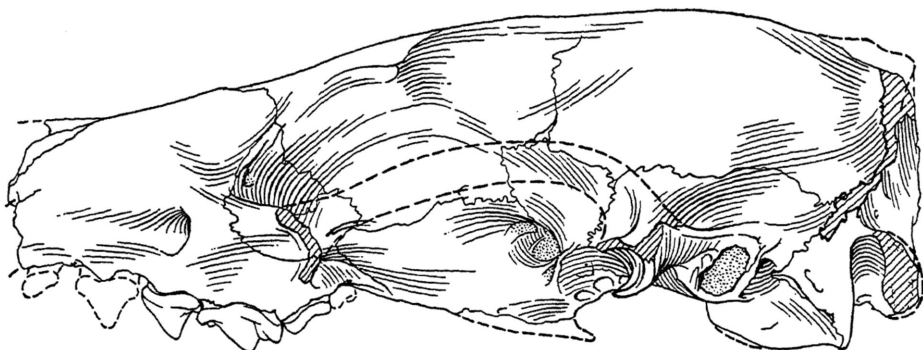


FIG. 22. *Viverra zibetha expectata*, new subspecies. Type, A.M.N.H. No. 18725, partial skull. Left lateral view. Natural size.

bone. These are considered individuals of a relatively recent date that fell into certain pits at Yenchingkou, to become commingled with the truly fossil specimens.

VIVERRIDAE

VIVERRA LINNAEUS

Viverra LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, pp. 43-44.

GENERIC TYPE: *Viverra zibetha* Linnaeus.

DIAGNOSIS: Large civets with elongated skull, strong zygomatic arches, prominent postorbital processes, and small bullae. Canine long and slightly compressed, first premolar small, P^4 sectorial, with large antero-internal cusp. Two molars. Upper molars transversely broad, lower molars with high trigonid and basined talonid.

Viverra zibetha expectata, new subspecies

TYPE: A.M.N.H. No. 18725, a skull, lacking the muzzle in front of the premolars, the zygomatic arches, and portions of the occiput and the right entotympanic.

PARATYPES: A.M.N.H. Nos. 18726, a right maxilla with P^2 - M^2 ; 18390, a right mandibular ramus with P_3 - M_2 (figured by Matthew and Granger, 1923, p. 586, as *Viverra* sp.)

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Similar to the modern form, *Viverra zibetha ashtoni*, in size and structure, but distinguished by the heavier muzzle and broader palate, the slightly larger auditory bulla, the somewhat more robust premolars, and the slightly lesser lingual extension of the first upper molar.

DISCUSSION

Viverra zibetha expectata, so far as size goes, is very close to the modern civet of Szechwan, *Viverra zibetha ashtoni*. This is a case in the Szechwan fossil fauna in which the extinct type is not definitely larger than its modern counterpart. The fossil is characterized by its elongated skull and expanded brain case, with a low sagittal crest. As mentioned in the diagnosis, this extinct type is distinguished by its relatively heavy muzzle, accompanied by a corresponding broadening in the anterior portion of the palate. It would seem, too, that there perhaps is less postorbital constriction in the fossil than is shown by the recent animal. The occiput is rather

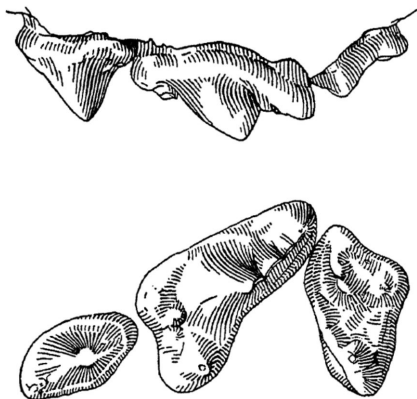


FIG. 23. *Viverra zibetha expectata*, new subspecies. Type, A.M.N.H. No. 18725, left P^3 - M^1 . Lateral and crown views. Twice natural size.



FIG. 24. *Viverra zibetha expecta*, new subspecies. A.M.N.H. No. 18726. Right maxilla with P²-M². Crown view. Twice natural size.

narrow and triangular as in the modern oriental civet, while the correspondence in the basicranial region between the fossil civet from Szechwan and the recent related form is close, about the only difference being the somewhat larger auditory bulla in the extinct form.

Few differences can be seen in the dentition. The premolars in the fossil are relatively heavy, although generally speaking the carnassial and molar teeth, as seen in the

type specimen, are somewhat less robust than in the modern civet. The smaller size, both actually and relatively, of the first upper molar in the fossil seems to be a real distinction and is noticeable in the lesser inward extension of this tooth in the Szechwan specimens than is the case among modern representatives of this genus and species.

Because of the above differences in a comparison of the fossil materials from Szechwan with modern specimens, a justifiable sub-

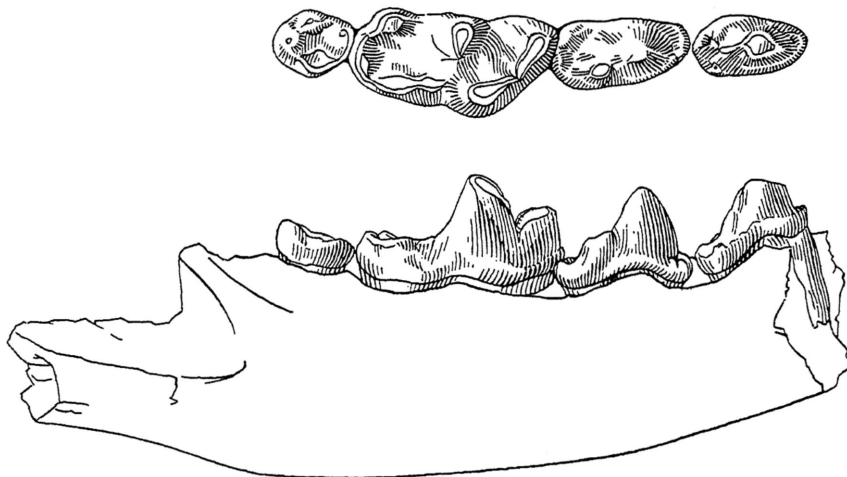


FIG. 25. *Viverra zibetha expecta*, new subspecies. A.M.N.H. No. 18390, right mandibular ramus with P₃-M₂. Crown and lateral views. Twice natural size.

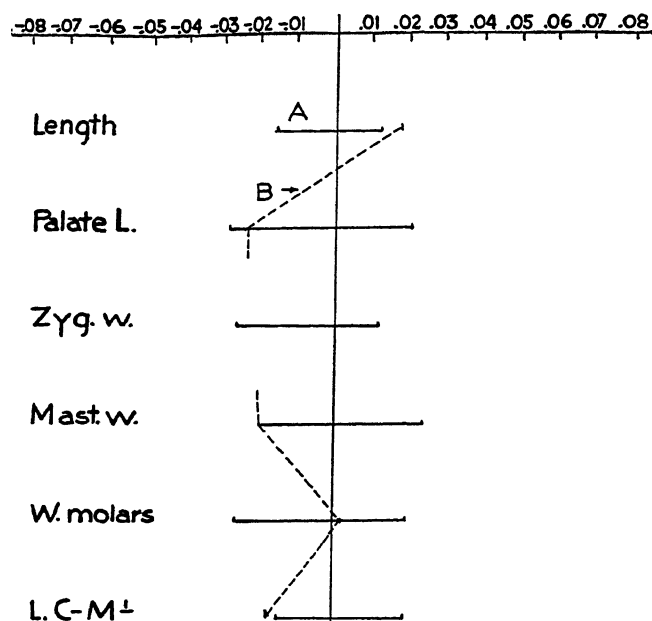


FIG. 26. Ratio diagram of comparative measurements.
A. *Viverra zibetha ashtoni*. B. *Viverra zibetha expecta*,
A.M.N.H. No. 18725.

TABLE 17
MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF *Arctonyx collaris*

	<i>A. c. rostratus</i>								<i>A. c. collaris</i>							
	A.M.N.H. No. 18381	A.M.N.H. No. 18382	A.M.N.H. No. 18722	A.M.N.H. No. 18718	A.M.N.H. No. 21781	A.M.N.H. No. 18393 ^a	A.M.N.H. No. 18394		A.M.N.H. No. 18716	A.M.N.H. No. 18719	A.M.N.H.(M.) No. 87394	A.M.N.H.(M.) No. 41475	A.M.N.H.(M.) No. 57373	A.M.N.H.(M.) No. 84391	A.M.N.H.(M.) No. 45296	
Length																
Premaxilla-condyle	—	—	—	175	154	150	—		151	145e	165	149	144	134	120e	
Palatal	—	—	—	131	111	111	—		106	—	117	105	102	94	80e	
Preorbital	—	—	—	71	61	62	—		58	—	63	57	54	50	44	
Postorbital	—	—	106	110	93	88	82		93	—	102	92	90	85	76	
Ramus	97.5	90e	—	117	107	—	—		99	—	109.5	97	96	89	80e	
Width																
Zygomatic	—	—	—	111	94	—	—		86	—	94	78.5	75	89	80.5	
Occipital	—	—	82	85	70	68	60e		70	—	76	65	57	64	59	
Postorbital constric- tion	—	—	39	42	36	34.5	35		35.5	—	38	37.5	35	39	30	
Brain case	—	—	57	60	53	50	51		50	—	53	50	49	51	47	
Palate at M ¹	—	—	—	27	24	20	—		26	—	27	24	22	23	21.5	
Height																
Occipital	—	—	48	50e	46	43	39		49	—	48	43	44	39	38	
Ramus at M ₁	16	13	—	22	17.5	—	—		15	—	17	15.5	15.8	14.5	13.5	

^a Type.

TABLE 18
LENGTH-BY-WIDTH DIMENSIONS OF THE UPPER TEETH OF *Arctonyx collaris*

	I ¹	I ²	I ³	C	P ¹	P ²	P ³	P ⁴	M ¹
<i>A. c. rostratus</i>									
A.M.N.H. Nos.									
18718	—	—	—	9.8×6.5	—	—	—	10.3×8.2	20.0×12.9
21781	3.0×—	3.9×—	6.3×—	9.5×5.5	—	5.3×—	7.3×—	9.6×—	18.0×12.0
18393 ^a	—	—	8.3×4.0	—	—	—	—	10.2×8.7	16.0×10.6
<i>A. c. collaris</i>									
A.M.N.H. Nos.									
18716	3.3×3.2	4.0×3.0	7.8×3.5	—	—	5.5×2.5	6.6×3.2	8.9×5.8	13.6× 8.7
18719	—	—	—	—	2.0×1.2	4.4×2.4	5.8×3.2	9.0×6.4	14.3×10.0
A.M.N.H.(M.) Nos.									
87394	—	—	—	9.3×5.2	—	—	—	9.0×6.4	14.2× 9.5
41475	—	—	—	8.5×5.8	—	—	—	10.0×8.4	17.8×12.2
53773	2.9×3.1	4.0×3.1	7.7×4.0	9.5×5.5	2.3×1.6	5.3×3.1	6.3×3.8	9.0×7.0	16.5×11.5
84391	2.9×3.0	3.9×3.0	7.6×4.0	9.6×5.7	2.4×1.1	5.2×2.8	6.7×2.9	9.2×8.7	17.0×11.2
45296	—	—	—	—	—	3.6×2.2	6.0×3.1	8.5×5.6	13.3× 9.6

^a Type.

specific separation is hereby considered to exist.

At the risk of being unduly repetitious we quote the description of the form under consideration from the original manuscript left by Matthew: "*V. expectata* [Matthew considered this a distinct species] of about the same size [as *V. zibetha* from China] but more robust throughout, broader palate and muzzle, larger bulla, heavier glenoid, etc. The premolars are more massive, p₁

considerably larger, p^3 with trace of inner cusp. P^4 has the parastyle much more developed, the protocone (inner cusp) is opposite it and not extended anterointernally as in the modern species, and it has no antero-internal cingulum. [These last distinctions are not considered sufficiently marked to be diagnostic.] M^1 , although wider anteroposteriorly, is less extended transversely, the internal cingulum being rudimentary. M^2 , preserved in No. 18726, is larger and wider

TABLE 19
LENGTH-BY-WIDTH DIMENSIONS (IN MILLIMETERS) OF THE
LOWER TEETH OF *Arctonyx collaris*

[illegible]

TABLE 20
MEASUREMENTS (IN MILLIMETERS) OF *Viverra zibetha*

	<i>V. z. expectata</i>			<i>V. z. ashtoni</i> 20 specimens
	A.M.N.H. No. 18725	A.M.N.H. No. 18726	A.M.N.H. No. 18390	
Length	145e	—	—	130.0–143.0
Palatal length	68e	—	—	63.3– 75.2
Width across molars	42.0	—	—	38.5– 43.7
Zygomatic width	—	—	—	62.8– 69.0
Mastoid width	41.5	—	—	41.5– 46.0
C–M ² , L	53e	—	—	50.0– 57.8
P ⁴				
L	13.4	14.3	—	12.1– 14.5
W	8.3	8.0	—	6.9– 8.3
M ¹				
L	7.0	7.8	—	6.3– 8.1
W	11.5	12.6	—	10.3– 13.1
M ₁				
L	—	—	13.5	12.3– 14.6
W	—	—	6.6	5.7– 7.2
M ₂				
L	—	—	5.4	4.8– 7.1
W	—	—	4.3	3.9– 5.7

anteroposteriorly than in the modern species. [This character does not hold on comparison with a sufficiently adequate series of modern animals.] In all the above characters the fossil species is less aberrant than its modern successor in its departure from the typical and more primitive viverrines of the later Tertiary."

HYAENIDAE

CROCUTA KAUP

Crocota KAUP, 1828, Oken's Isis, vol. 21, no. 11, p. 1145.

GENERIC TYPE: *Canis crocuta* Erxleben.

DIAGNOSIS: Large hyenids, with a shortened facial region and a high sagittal crest. Third upper incisor much larger than the other incisors; posterior premolars large and strong, P⁴ much elongated; M¹ at right angles to last upper premolar, large in primitive members of the genus but tending to become progressively smaller. First lower molar progressively lengthening, with metaconid absent or vestigial and talonid reduced to a very small, trenchant element—a distinct contrast to *Hyaena* in which the talonid is relatively large and basined; M₂ absent.

Crocota crocuta sinensis (Owen)

Hyaena sinensis OWEN, 1870, Quart. Jour. Geol. Soc. London, vol. 26, pp. 422–424.

Hyaena ultima MATSUMOTO, 1915, Sci. Repts. Tôhoku Imp. Univ., ser. 2 (geol.), vol. 3, no. 1, pp. 2–3.

Crocota sinensis, PILGRIM, 1932, Palaeont. Indica, new ser., vol. 18, pp. 138 ff.

Crocota ultima, PILGRIM, loc. cit.

Hyaena zdanskyi PEI, 1934, Palaeont. Sinica, ser. C, vol. 8, no. 1, pp. 110–116.

COTYPES: B.M. Nos. 41937, right third upper premolar; 41938, right third lower premolar; 41939, lower canine.

REFERRED SPECIMENS: A.M.N.H. Nos. 18392, portion of left premaxilla and maxilla with third incisor and bases of canine and anterior premolars; 18395, fragments of right maxilla and right mandible, with P³⁻⁴ and P₄, M₁, much worn, also roots of anterior upper premolars; 18396, fragment of left mandibular ramus with P₃₋₄; 18397, fragment of right mandibular ramus with P₃₋₄, also a right P₃, left P₄, and miscellaneous fragments; 18730, associated skull and jaw. The skull lacks a portion of the premaxillaries, the left zygomatic arch, part of the cranium, and the occipital condyles and

auditory bullae. Of the upper dentition the right C, P¹⁻⁴ are present, the other teeth being represented by broken roots. In the jaw, the left ramus is missing behind the fourth premolar. The lower dentition lacks the incisors and the left carnassial. A.M.N.H. No. 18732, a partial skull. The occiput, zygomatic arches, most of the left maxillary, and the anterior portion of the premaxillaries are missing. Of the dentition, only the canine and the cheek teeth of the right side remain, and these are badly mutilated. A.M.N.H. Nos. 18734, right mandibular ramus of a juvenile with the deciduous cheek teeth; 21795, maxilla fragment with left P³, P⁴ (broken); 39217, left P⁴.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China. Also found in adjacent provinces in deposits of Pleistocene age.

DIAGNOSIS: A large, robust *Crocota*, characterized by its relatively large, heavy cheek teeth, especially those of the premolar series.

DISCUSSION

A number of specimens, including a rather good skull and mandible and another skull only partially preserved, give us additional knowledge of the hyena from the Szechwan pits, first described by Owen.

These specimens are significant because of their large size and robustness as compared with the modern *Crocota crocuta* from Africa. In all respects the fossil hyenid from Szechwan resembles the modern African form rather than the true *Hyaena* from India, for it shows the same advanced characters, particularly those of the dentition, which characterize *Crocota*. This resemblance is not surprising, since most of the Pliocene and Pleistocene hyenids of Asia belong to the *Crocota* group, a point ably demonstrated by Pilgrim and other authors.

The Szechwan species is distinguished not only by its large size but also by the great size and robustness of its teeth, particularly the posterior premolars and the carnassials. These teeth are both actually and relatively (in comparison to the size of the skull) larger than the comparable elements of the dentition in the African hyena. With this exception, there are few qualitative differences of any great importance between the fossil

type and the modern species from Africa. Certain differences of proportion are apparent, it is true, but these are not large, and many of the supposed proportional differences prove on analysis to be the result of a harmonic increase of the part in question, due to the general increment in size that characterizes the Yenchingkou hyena.

Therefore it seems evident that the differences between the fossil hyena of Szechwan and the modern African species and likewise those between the fossil and other alleged fossil species from China are not so great as has been argued by certain authors, notably Matsumoto, Zdansky, and Pei. This question is considered in detail below.

Various authors have described Pleistocene hyenids from China, with the result that several species have been proposed, the relationships of which are at the present time in a state of great confusion. The question of the nomenclature of the Chinese Pleistocene hyenids is considered below. What concerns us here is the question of whether one or two species is to be recognized from the Pleistocene of Szechwan. Owen described *Hyaena sinensis* in 1870 on the basis of some premolar teeth. Should Matsumoto's species, *Hyaena ultima*, named in 1915 on the basis of a single upper carnassial be recognized as a separate form, particularly in view of the fact that it came, as did Owen's species, from the province of Szechwan?

Matsumoto distinguished *Crocota ultima* from *Crocota sinensis* because of the large size of its upper carnassial and because of the long cutting blade on this tooth. Zdansky, working with a good series of referred material, corroborated Matsumoto's distinction and in addition postulated that the later-named form can be distinguished by its large premolars, by the relatively great size of the third lower premolar as compared with the fourth lower premolar (stipulating that in *Crocota sinensis* these teeth are more nearly equal to each other), and by the rather long first lower molar. These distinctions were supported by Pei in 1934.

Since a distinction of two forms has been made, on the basis of the characters outlined above, it was thought advisable to test this distinction by a comparison with a series of modern hyenids belonging to a single

species. Eighteen skulls, jaws, and dentitions of *Crocota crocuta* were measured, in order to compare them with the Pleistocene hyenids from China. Of these, 10 individuals came from one locality, thereby giving us some clue as to the degree of variation in a single population of the modern spotted hyena. The eight remaining individuals came from various localities in Africa. The African hyena was used in this comparative study because of its obvious relationship with the Pleistocene hyenids from China. Measurements of the fossil and recent forms are given in tables 21 to 25.

Our special problem was to test the conclusions of Matsumoto, Zdansky, and Pei with regard to the validity of *Crocota ultima* as distinguished from *Crocota sinensis* on the basis of the characters of P_4 , the relative size of P_3 and P_4 as compared with M_1 , and the size of P_3 as compared with P_4 .

In table 23 the length of the blade (metacone plus metastyle) is compared with the length of the upper carnassial. It can be seen that these attributes in the carnassial of the modern hyena from a single locality form a rather uniform series, while in modern hyenas from scattered localities the series is slightly less uniform, as might be expected. If, then, all the Chinese Pleistocene hyenas on which measurements of P_4 were available be considered, it is at once apparent that taken together these form a more variable series than the individuals of the modern species—again a result that might have been expected, *a priori*. But if the Pleistocene specimens be examined quite objectively, it is difficult to make any very good distinction between them on the basis of carnassial length or blade length. The specimens from Szechwan seem to have greater carnassial dimensions than many of the other Pleistocene specimens from other parts of China, but this is not invariably the case. Therefore, on the basis of the limited evidence at hand, it seems probable that no valid distinction can be made between the Chinese hyenids heretofore assigned to the two species, on the evidence of the dimensions or proportions of the upper carnassial.

Table 24 shows the difference between the combined length of the last two lower premolars and that of the lower carnassial.

Here, as in table 23, the data indicate a greater uniformity in the series of modern specimens than in the fossils, and among the modern animals, those from a single locality are perhaps slightly more uniform in these comparative lengths than those from scattered localities—all of which results conform to the expected conclusions. It is interesting to notice that whereas the carnassial tooth in the fossils is not much different in length from that in recent hyenas, the premolars in the fossils are considerably larger than those of the recent animals. This reinforces the conclusion, drawn from a simple examination of the specimens, that all Pleistocene hyenids from China had relatively larger premolars than the recent African animal. But here again, as in the case of the upper carnassial, there seems to be little if any evidence for a difference in the fossil material between those specimens (in this case a single specimen) from Szechwan and those from other provinces.

This comparison may be completed by a study of the breadth of the last two lower premolars. Here again, tables 21 to 25 show that although the premolars in the fossils are larger than those of the recent spotted hyena, the relative differences between P_3 and P_4 are about the same throughout. In some of the material referred by Zdansky and by Pei to *C. sinensis*, the last two lower premolars seem to be more nearly equal in breadth (a character designated by Zdansky as distinctive for this species) than in the fossils from Szechwan. But on the other hand, in one of the specimens identified by Zdansky as *C. ultima*, supposedly with a P_4 much narrower than the adjacent P_3 , these two teeth are of equal width. Moreover the degree of variability in this width relationship as shown by *C. crocuta* from a single locality seems to indicate that the differences observed in the fossils are without any very special significance.

Therefore, from the analysis of dental characters which had been cited by previous authors (Matsumoto, Zdansky, Pei) as the bases for a differentiation of at least two separate species from the Pleistocene of China, it is hereby suggested that no true dichotomy exists, but rather that all or most of the material heretofore separated into two species,

Hyaena sinensis and *Hyaena ultima*, constitutes a single form, the name of which should be *Crocota crocota sinensis* (Owen). These conclusions are borne out, in so far as it is possible to make definite decisions based on the uniformly developed skull structures in the genus *Crocota*, by the similarity in size and form of the skulls and jaws among the fossil materials from the Middle Pleistocene of China.

In this connection it is also suggested, even though not pertinent to the present investigation, that the species distinguished by Pei as *Hyaena zdanskyi* represents merely a juvenile stage in the hyena from Choukoutien, whatever that form may be. By a comparison of Pei's species with a series of spotted hyenas, it is at once evident that the characters cited by this author as distinctive (small, short "swollen" skull, small postorbital processes, faint sagittal crest, etc.) are those characteristic of a juvenile *Crocota*. When one considers, in addition, that the type speci-

men of *H. zdanskyi* shows the permanent dentition in process of eruption, the conclusion as presented above attains additional weight.

A TAXONOMIC REVIEW OF *Crocota crocota sinensis* AND *Crocota ultima*

Hyaena sinensis was described by Owen in 1870 on the basis of an upper and a lower third premolar, and a broken canine, all of which came from a cave near "Chung-king-foo" in the province of Szechwan. Owen compared his material with comparable teeth in the three types of modern hyenas and with the fossil hyenas then known from the Siwalik beds of India and from the caves of Europe, and arrived at the conclusion that the Chinese fossil was distinct from any other species with which it might be compared because of its relatively large, but low, third premolars in both jaws. Obviously this comparison, valid as it might be, was based on relatively incomplete evidence.

TABLE 21
MEASUREMENTS (IN MILLIMETERS) OF SKULL AND UPPER TEETH OF *Crocota crocota*

	<i>C. c. sinensis</i>			<i>C. crocota</i>
	A.M.N.H. No. 18730	A.M.N.H. No. 18732	A.M.N.H. Nos. 18392, 18395	A.M.N.H.(M.) No. 54312
Length				
Premaxilla-condyle	225a	260a	—	211.5
Palatal	120a	—	—	108
Preorbital	80a	95a	—	79.5
Postorbital	145a	165a	—	132
Width				
Zygomatic	152	—	—	139
Occipital	96	132	—	89.5
Postorbital constriction	42	49	—	42
Brain case	83	90	—	73
Palate at M ¹	90	100	—	77.3
Height				
Occipital	77a	109	—	71
L×W				
I ¹	—	—	—	5.3×6.3
I ²	—	—	—	6.2×7.9
I ³	13.3×9.5	—	13.0×10.6	8.3×10.5
C	17.0×13.0	20.5×14.5	19.7×13.4	14.9×11.1
P ¹	6.2×6.5	—	—	8.3×7.2
P ²	17.3×14.0	18.5×13.2	—	14.0×10.3
P ³	22.5×18.7	24.3×18.0	24.5×17.5	19.4×14.5
P ⁴	42.0×22.0	—×19.5	39.0×21.5	35.2×19.8
M ¹	—	—	—	4.2×3.4

TABLE 22

MEASUREMENTS (IN MILLIMETERS) OF JAWS AND LOWER TEETH OF *Crocota crocuta*

	A.M.N.H. No. 18730	<i>C. c. sinensis</i> A.M.N.H. No. 18395	A.M.N.H. No. 18396	<i>C. crocuta</i> A.M.N.H.(M.) No. 54312
Length of ramus	174.0	—	—	159.0
Depth of ramus, M ₁	37.5	—	—	34.0
L×W				
I ₁	—	—	—	3.5×4.7
I ₂	—	—	—	5.2×6.3
I ₃	—	—	—	7.8×7.2
C	16.5×14.0	—	—	13.5×10.0
P ₂	16.0×12.0	—	—	13.9×9.1
P ₃ ^a	22.0×17.0	21.8×17.2	24.0×16.3	18.7×12.6
P ₄	25.0×15.0	23.8×16.2	24.1×15.3	21.0×10.8
M ₁	31.7×13.0	30.0×13.2	—	25.6×10.0

^a In A.M.N.H. No. 18397, 24.5×18.8.

In 1885, Koken described additional hyenid teeth from China, attributing them to Owen's species. This material, which came from Yunnan, contained incisors, premolars, and carnassials. Supposing his material to be conspecific with the type, Koken thereby established additional characters distinctive for *Hyaena sinensis*.

In 1903 Schlosser discussed this species but made no new contribution to its anatomy or taxonomic position.

Then in 1915 a series of fossils from Szechwan was described by Matsumoto. In this new lot of material there was an upper carnassial of a hyena, which Matsumoto distinguished as a new species, *Hyaena ultima*. Naturally it was impossible for Matsumoto to compare the single fourth premolar, which constituted the type for his species, directly with the type of *Hyaena sinensis*, so he was forced to make his comparison with the referred material described by Koken in which there were some carnassial teeth. On the basis of this comparison he characterized his new species as distinct from *Hyaena sinensis* by virtue of the greater size of its carnassial, with a relatively reduced anterior lobe (paracone), an elongated shear, and an anteriorly situated protocone.

Matthew and Granger, in 1923, identified the fossils in the American Museum collection from Szechwan as belonging to Owen's species, but beyond this they made no re-

marks on the anatomy or the relationships of the form or forms represented by fossils from Szechwan.

It remained, therefore, for Zdansky to discuss the two species in detail, in his papers of 1925 (1925a) and 1927. Working with far more complete material than had hitherto been described, including skulls and jaws, this author set forth the characters that he considered as distinctive of *Hyaena sinensis* and of *Hyaena ultima*. He followed Matsumoto in distinguishing *Hyaena ultima* from *Hyaena sinensis* because of its larger premolars and its longer carnassial shear, in this case in both the upper and the lower teeth. In addition, Zdansky decided that whereas the third and fourth lower premolars in *Hyaena sinensis* are of approximately equal breadth, the posterior tooth is considerably narrower than the anterior one in *Hyaena ultima*. In short, Zdansky recognized *Hyaena ultima* as a form more specialized than *Hyaena sinensis*, regarding this latter as a form more or less closely related to the modern *crocota* type.

In 1932, Pilgrim, recognizing the close relationships of the Chinese Pleistocene hyenas with the modern African forms, placed the fossils in the genus *Crocota*. Finally, Pei in 1934, in connection with his monograph on the carnivores from Choukoutien, discussed in some detail the extinct hyenids of China. On the basis of a great quantity of

TABLE 23
P⁴ IN *Crocota crocuta*

	Length of P ⁴	Length of Blade
<i>C. c. sinensis</i>		
A.M.N.H. No. 18730	42.0	32.5
From Koken	39.0	26.0
From Koken	38.2	27.0
From Matsumoto (<i>C. ultima</i>)	42.0	35.0
From Zdansky (<i>C. ultima</i>)	42.8	33.0
From Zdansky (<i>C. ultima</i>)	40.0	30.0
From Zdansky (<i>C. ultima</i>)	39.6	26.7
Range of Variations		
<i>C. c. sinensis</i>		
7 specimens (above)	38.2-42.8	26.0-35.0
<i>C. crocuta</i>		
7 specimens, various localities	34.5-39.0	26.5-31.6
10 specimens, Faradje	35.6-38.7	27.5-29.9

new material (not coming from the type localities) he further redefined the two species in question, and came to the following conclusions:

1. Owen's species is "not valid" because it is insufficiently defined. Therefore *Hyaena sinensis* should be based on the redefinition as presented by Zdansky. (Pei goes so far as to designate this form *Hyaena sinensis* Zdansky.)

2. The hyena from Szechwan is *Hyaena ultima* Matsumoto. However, Owen's material may belong to the same species as that of Matsumoto.

3. Koken's specimens are different from *Hyaena ultima*. Pei regards these as belonging to a southern race of *Hyaena sinensis*.

There can be no doubt but that Owen described *Hyaena sinensis* on the basis of incomplete and insufficient material. But the description was properly made, and all subsequent references must go back ultimately to this type description. Where Matsumoto erred was in comparing his new specimen with the referred material described by Koken. Obviously no direct comparison could be made with Owen's types, since homologous parts were not involved, but for Matsumoto

TABLE 24
P₃+P₄, M₁ IN *Crocota crocuta*

	Length of P ₃ +P ₄	Length of M ₁
<i>C. c. sinensis</i>		
A.M.N.H. No. 18730	47.0	31.7
From Zdansky	48.7	26.7
From Zdansky	49.8	27.7
From Zdansky (<i>C. ultima</i>)	50.5	35.5
From Zdansky (<i>C. ultima</i>)	52.6	30.6
From Pei	54.0	28.3
From Pei	51.3	29.6
From Pei (<i>C. ultima</i>)	48.6	31.4
Range of Variations		
<i>C. c. sinensis</i>		
8 specimens (above)	47.0-54.0	26.7-35.5
<i>C. crocuta</i>		
7 specimens, various localities	39.9-45.4	25.7-31.1
10 specimens, Faradje	41.7-44.7	24.5-29.5

to assume, without critically reviewing the question, that Koken's specimens were absolutely conspecific with the type and then to differentiate his new species on the basis of such an assumption was an error in procedure that was bound to confuse the issue for subsequent authors. *A priori*, since Koken's specimens came from a locality far removed from that for the type, while Matsumoto's specimen came from some place reasonably close to the type locality, one might be justi-

be *Hyaena sinensis*, with Matsumoto's form *Hyaena ultima* assuming the role of a synonym.

On the basis of the present independent study of the fossils as described by these various authors and of a careful examination of the new material from Yenchingkou described herein, certain conclusions with regard to the Pleistocene hyenas of China have been reached. These are:

1. There is every reason, as shown in the

TABLE 25
WIDTHS OF P₃ AND P₄ IN *Crocota crocuta*

	P ₃	P ₄
<i>C. c. sinensis</i>		
A.M.N.H. No. 18730	17.0	15.0
A.M.N.H. No. 18396	16.3	15.3
A.M.N.H. No. 18397	17.2	16.2
From Zdansky	17.0	17.1
From Zdansky	17.2	16.8
From Zdansky	16.4	16.0
From Zdansky (<i>C. ultima</i>)	18.6	18.6
From Zdansky (<i>C. ultima</i>)	18.5	16.3
From Pei	18.0	17.1
From Pei	17.0	18.0
From Pei	17.2	15.3
Range of Variations		
<i>C. c. sinensis</i>		
11 specimens (above)	16.3-18.6	15.0-18.6
<i>C. crocuta</i>		
7 specimens, various localities	13.5-15.8	11.2-13.8
10 specimens, Faradje	13.5-16.0	11.0-13.6

fied in supposing that it would be Matsumoto's specimen that could be identified with Owen's type, not Koken's.

This confused situation was perpetuated by Zdansky in his redefinition of the two species.

Lastly, Pei made a thoroughly unwarrantable assumption in supposing that Owen's species was "not valid" because it was founded on poor material. The species is valid by the rules of zoological nomenclature, and the fact that its type is not so complete as it might be does not alter the situation. Consequently, Pei is not in the least justified in designating this form as *Hyaena sinensis* Zdansky. Furthermore, if the hyena from Szechwan belongs to a single species, as is intimated by Pei, then the designation must

comparative studies, to think that the materials described by Owen in 1870 and those described by Matsumoto in 1915 belong to a single species, particularly in view of the fact that Matsumoto distinguished his species on the basis of a comparison with referred material from a locality far removed from the type locality.

2. The name of this species of hyena from the Middle Pleistocene of Szechwan is *Crocota crocuta sinensis* (Owen). *Crocota ultima* (Matsumoto) is here considered a synonym of *Crocota crocuta sinensis*.

3. All the Middle Pleistocene hyenids from various Chinese provinces probably belong to this single species. However, if the material described by Koken from Yunnan is different from that of Szechwan, then it is at pres-

ent without a specific designation. The same holds true for the materials described by Zdansky from Honan and other localities, and by Pei from Choukoutien.

4. The following taxonomic and stratigraphic relationships are hereby suggested for the Chinese Hyaenidae:

Upper Pleistocene	<i>Crocota spelaea</i> : Sjara-osso-gol in Ordos
Middle Pleistocene	<i>Crocota crocota sinensis</i> : Yenchingkou, Szechwan; Honan, Shansi, Yunnan, Hopei Syn. <i>C. ultima</i> <i>C. zdanskyi</i> : Choukoutien, Hopei
Lower Pleistocene	<i>Crocota licenti</i> : Nihowan
Pliocene	<i>Crocota variabilis</i> : Pontian, Hipparion beds, Shansi, Shensi, Kansu Syn. <i>C. honanensis</i> : Pontian, Honan <i>Crocota gigantea</i> : horizon and locality unknown

FELIDAE

FELIS LINNAEUS

Felis LINNAEUS, 1758, Systema naturae, ed. 10, vol. 1, p. 41.

GENERIC TYPE: *Felis catus* Linnaeus.

DIAGNOSIS: Highly specialized felids in which there are two or three upper premolars, two lower premolars, and a single molar, above and below. Carnassials with long cutting blades. Mastoid process small and pressed against bulla. No flange on lower jaw.

Felis tigris Linnaeus

Felis tigris LINNAEUS, 1758, Systema naturae, ed. 10, vol. 1, p. 41.

Felis aff. *tigris* MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 584.

Panthera tigris (Linnaeus) subspecies, HOOIJER, 1947, Amer. Mus. Novitates, no. 1346, p. 1.

REFERRED SPECIMENS: A.M.N.H. Nos. 18448, right humerus, femur, and tibia, unassociated; 18451, upper C and skull fragment; 18452, right mandibular ramus with P_4 , M_1 ; 18472, right mandibular ramus with DC, DM_{3-4} , M_1 (in alveolus); 18624, skull and mandible, virtually complete and associated; 18671, right metatarsals II and III; 18672, left metacarpals II-V, probably associated; 18673, right mandibular ramus with P_2 - M_1 , left mandibular ramus with P_4 - M_1 , probably associated; 18674, left metatarsal IV; 18675, left metatarsal IV; 18676, right premaxillary fragment, with I^3 , one right and one left P^4 , left lower C, one right and one left M_1 ; 18677, four upper C; 18678, right P^4 , right lower C, fragment of right mandibu-

lar ramus with P_3 , P_4 (broken), right P_4 , left M_1 ; 18679, fragment of right maxilla with C, P^{2-3} , right P^4 , left lower C, left P_3 , fragment of right mandibular ramus with P_4 , M_1 ; 18680, left upper C, left P^3 , maxillary fragment with right P_4 , left lower C, left P_4 , frag-

ment of right mandibular ramus with M_1 ; 18681, three right and two left metacarpals IV; 18687, one right and four left metacarpals III; 18688, right metacarpals II-V, probably associated; 18689, left calcaneum; 18690, left calcaneum; 18691, left astragalus; 18692, three left and one right metacarpals II; 18693, one right and two left metacarpals V; 18694, two left metatarsals III; 18695, two left metatarsals IV; 18696, left metatarsal IV; 18697, left metatarsals II-V, probably associated; 18698, four right metatarsals III; 18699, three right metatarsals II; 18700, left metatarsal V; 18737, front of skull and associated mandible; 18738, three maxillary fragments, with left DC, DM^3 , P^4 (erupting), with right DM^3 , and with right DC, P^2 , and two mandibular rami with incisors, right DM_{3-4} , M_1 erupting, and with right DM_{3-4} ; 18740, left mandibular ramus with C- M_1 ; 18741, left maxilla with P^{3-4} , and left mandibular ramus with P_{3-4} , M_1 ; 18743, right mandibular ramus with P_{3-4} , M_1 ; 21779, left mandibular ramus with P_{3-4} , M_1 , and fragments of right ramus with P_3 and with M_1 ; 39218, left premaxilla with I^{2-3} ; 39219, right metacarpal III.

C.N.H.M. Nos. P.14145, left maxilla with P^{3-4} , and left mandibular ramus with P_{3-4} , M_1 ; P.14146, fragment of left mandibular ramus with P_4 , M_1 ; P.14147, right P^4 .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Large felines with heavy forequarters. Forehead elevated and nasal bones comparatively long. Lower profile of mandible concave.

TABLE 26
MEASUREMENTS (IN MILLIMETERS) OF THE UPPER TEETH OF *Felis tigris*

	C		P ³		P ⁴	
	L	W	L	W	L	W
<i>Felis tigris</i>						
A.M.N.H. Nos.						
18624	—	—	19.3	10.5	33.3	—
18741	—	—	24.5	13.0	38.1	19.9
18679	32.7	23.4	26.8	14.2	37.5	19.8
18680	32.5	23.7	23.0	12.4	37.8	21.4
18678	—	—	—	—	42.0	22.0
18677	31.7	23.1	—	—	—	—
18677	28.4	21.1	—	—	—	—
18451	29.4	22.4	—	—	—	—
C.N.H.M. Nos.						
P.14145	—	—	27.6	—	37.6	—
P.14146, P.14147	—	—	—	—	37.4	20.3
<i>F. t. tigris</i>						
A.M.N.H.(M.) Nos.						
54458	26.6	19.7	23.0	11.8	35.9	18.5
54459	27.1	20.0	23.8	12.4	36.1	18.5
90016	24.1	16.5	21.5	10.7	34.4	17.3
113748	20.9	15.2	20.5	11.1	33.1	16.0
119680	23.8	18.0	21.0	10.4	35.0	17.3
87348	—	—	22.5	11.3	35.1	17.2

DISCUSSION

The Yenchingkou tiger is seemingly indistinguishable specifically from the recent *Felis tigris*, as was pointed out by Matthew and Granger (1923, p. 584). Several years ago one of us (Hooijer, 1947a) made a comparative study of certain specimens that had been sent to Leiden, Netherlands, on a loan, including the skulls A.M.N.H. Nos. 18624 and 18737, some lower jaws, and limb and foot bones. Now it is clear that there are no differences between the skulls of the Yenchingkou fossils and those of the recent tiger, but the teeth in the fossil specimens occasionally are larger than in the modern tiger. This was also observed by Young (1939, p. 320), who remarks upon a rather large upper canine of the tiger from Yenchingkou that has the root more robust and swollen than in any living tiger used for comparison.

The measurements of the Yenchingkou specimens are given in tables 26 and 27, with the tooth dimensions of a series of six skulls of *Felis tigris tigris* Linnaeus from India and Indo-China. It will be observed that most of the fossil teeth are larger than their recent

homologues, which belong to the largest of the living races of the tiger.

Pleistocene remains of the tiger that have been recorded from Choukoutien (Pei, 1934, p. 130; 1936, p. 52) are not especially large, but the mandible recorded as *Felis youngi* (Pei, 1934, p. 133) seems to be a large specimen of *Felis tigris*; it is not larger than some of the Yenchingkou specimens (Hooijer, 1947a, p. 2). Also among the Pleistocene tiger remains from Java recorded by Stremme (1911, p. 86), von Koenigswald (1933, pp. 6, 14), and Brongersma (1935, p. 51) are specimens that exceed the living tiger in size.

The measurements of some limb and foot bones (humerus, tibia, astragalus, and calcaneum) from the Yenchingkou collection have already been given in the earlier paper on the tiger from this locality (Hooijer, 1947a). Beyond a small excess in size over the recent specimens used for comparison there is nothing special to remark about these elements. In the metapodials, however, there is a character that distinguishes the fossil tiger from the recent, viz., the great massiveness of the fossil bones. Seven metapodials were

TABLE 27
MEASUREMENTS (IN MILLIMETERS) OF THE LOWER TEETH OF *Felis tigris*

	C		P ₃		P ₄		M ₁	
	L	W	L	W	L	W	L	W
<i>F. tigris</i>								
A.M.N.H. Nos.								
18624	—	—	14.9	—	22.8	—	—	—
18741	—	—	18.0	10.0	25.7	13.0	27.6	14.7
18679	25.0	19.1	18.7	10.5	25.9	13.1	27.0	14.6
18680	28.0	19.4	—	—	25.4	12.7	31.0	15.7
18678	31.5	22.9	18.8	10.4	28.8	14.5	30.8	16.0
18676	—	—	—	—	—	—	29.3	15.8
18676	25.9	18.6	—	—	—	—	26.7	14.6
18740	23.4	16.8	16.7	10.0	24.5	12.9	28.0	14.3
18743	—	—	16.9	8.8	22.8	12.0	24.7	12.9
21779	—	—	15.9	8.5	23.3	11.4	25.1	13.2
18452	—	—	—	—	22.5	11.0	25.5	12.5
18673	—	—	16.5	9.0	22.8	11.6	25.3	12.5
C.N.H.M. Nos.								
P.14145	—	—	18.0	9.5	28.0	14.2	29.5	15.1
P.14146, P.14147	—	—	—	—	26.6	13.8	29.0	14.6
<i>F. t. tigris</i>								
A.M.N.H.(M.) Nos.								
54458	23.2	18.0	16.1	7.7	22.8	11.1	26.4	12.9
54459	23.9	17.2	17.4	8.8	25.1	11.8	27.1	14.0
90016	22.4	15.4	15.3	7.3	23.3	10.5	25.2	12.0
113748	18.6	14.2	14.0	7.4	21.0	10.7	25.6	11.9
119680	22.5	15.4	14.8	7.3	22.8	11.0	25.4	12.6
87348	24.1	16.9	15.4	8.5	23.7	11.4	25.8	12.9

available for the earlier study (Hooijer, 1947a). Many more specimens have been subsequently examined, and the data are presented in table 28. The variation ranges given for the recent tiger are derived from nine recent tiger skeletons from various localities. It is clear that the majority of the fossil bones exceed the recent in their transverse and anteroposterior diameters, showing that the recent tiger metapodials are more slender than the Pleistocene bones.

No metapodials of the tiger have been described from Choukoutien, but Tscherski (1892, pp. 58–60, pl. 1, fig. 4) described a fossil metatarsal II from Lyakhov Island, off the north coast of Siberia, that is much thicker than recent tiger metatarsals II and agrees in that respect with the Yenchingkou specimens. On the other hand, the few tiger metapodials that are known from the Pleistocene of Java are not, or hardly, beyond the variation range of the recent bones (Hooijer, 1947a, p. 10). Such specimens are very rare

in the series from Yenchingkou. There is one set of metacarpals (A.M.N.H. No. 18672), probably associated, that falls within the recent limits and is shown in plate 15, contrasting with the common massive metapodials of Yenchingkou of which both a set of metacarpals and of metatarsals are shown.

The Yenchingkou tiger consequently is notable because of its large size, a character that it has in common with Pleistocene tigers from other localities. The difference is probably on the order of subspecific differentiation, and the metapodials suggest that there was some sort of geographic subspeciation already in the Pleistocene, with the Javan form showing a closer approach to the living tiger than to the Chinese or the Siberian tiger. We need much more material to distinguish eventually between various Pleistocene subspecies of *Felis tigris*¹ in southeastern Asia.

¹ *Panthera* Oken, 1816, used for the tiger in Hooijer (1947a) and earlier papers cannot be accepted as a technical name (Hershkovitz, 1949, p. 298).

TABLE 28
MEASUREMENTS (IN MILLIMETERS) AND INDICES OF METAPODIALS OF *Felis tigris*^a

A.M.N.H. Nos.	18692	18692	18692	18692	18688	18672		<i>F. t. tigris</i>
Metacarpal II								
1	104	98	97	100	100	90		81-104
2	26	24	24	25	24	21		17-22
3	34	32	33	—	34	27		23-27
4	17	17	17	16	17	13		11-12
5	26	25	25	26	26	—		17-20
6	25	24	25	25	24	23		20-24
7	33	32	34	—	34	30		25-30
A.M.N.H. Nos.	18693	18693	18693	18688	18672			
Metacarpal V								
1	87	80	94	87	81			70-90
2	26	20	24	25	20			16-23
3	26	21	28	25	23			19-24
4	16	12	15	16	12			10-13
5	22	20	23	22	18			17-19
6	30	25	26	29	25			23-26
7	30	26	30	29	28			25-28
A.M.N.H. Nos.	18699	18699	18699	18671	18697			
Metatarsal II								
1	116	116	113	101	102			93-116
2	—	19	18	15	15			13-17
3	32	33	33	28	28			23-26
4	16	15	15	12	14			10-13
5	24	24	26	21	22			17-20
6	—	16	16	15	15			14-17
7	28	28	29	28	28			22-26
A.M.N.H. Nos.	18698	18698	18698	18671	18694	18694	18697	
Metatarsal III								
1	132	128	118	116	119	127	128	107-130
2	28	28	25	23	25	27	27	21-25
3	37	38	35	33	35	36	38	27-31
4	19	20	18	15	17	20	20	12-15
5	27	28	24	23	—	28	27	19-24
6	21	22	21	20	21	21	21	18-20
7	28	30	30	28	29	28	30	24-27
A.M.N.H. Nos.	18696	18695	18695	18674	18675	18697		
Metatarsal IV								
1	130	128	119	118	119	128		108-130
2	28	28	25	23	23	28		19-23
3	34	33	30	27	25	33		23-28
4	18	17	16	14	13	18		10-13
5	25	24	22	21	20	25		18-21
6	22	22	21	19	19	22		16-20
7	26	26	25	23	21	26		20-25
A.M.N.H. Nos.	18697	18700						
Metatarsal V								
1	112	104						95-116
2	27	23						18-23
4	14	12						9-12
5	21	18						15-18
6	24	22						18-21

^a In this table the measurements are indicated by numbers: 1, median length; 2, proximal width; 3, proximal anteroposterior diameter; 4, smallest width of shaft; 5, distal width; 6, proximal width $\times 100$ /median length; 7, proximal anteroposterior diameter $\times 100$ /median length.

Felis sp.

SPECIMEN UNDER CONSIDERATION:
A.M.N.H. No. 21780, right mandibular ramus with P_4 , M_1 .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

A small cat in the Yenchingkou fauna is represented by the specimen listed above. Unfortunately, this fossil is not complete enough to be truly definitive, so that it can be identified only as one of the smaller species of cats, comparable in size to *Felis bengalensis* and similar forms. It is definitely smaller than *Felis pardus*. Its measurements (in millimeters) are: P_4 length, 11.6; P_4 width, 6.0; M_1 length, 13.7; M_1 width, 6.2; depth of ramus at M_1 , 19.3.

PROBOSCIDEA

STEGODONTIDAE

STEGODON FALCONER

Stegodon FALCONER, 1857, Quart. Jour. Geol. Soc. London, vol. 13, pt. 4, pp. 314, 318.

GENERIC TYPE: *Mastodon elephantoides* Clift.

DIAGNOSIS: A large proboscidean of late Pliocene and Pleistocene age, characterized by the crested molars, in each of which there are "low, roof-shaped, slightly convex, and usually multipapillose transverse crests, the intermediate valleys being partially filled with cement" (Zittel, 1925, vol. 3, p. 261). There are no tusks in the mandible.

Stegodon orientalis Owen

Stegodon orientalis OWEN, 1870, Quart. Jour. Geol. Soc. London, vol. 26, pp. 421-422, pl. 28, figs. 1-4.

Stegodon insignis, LYDEKKER, 1880, Palaeont. Indica, ser. 10, vol. 1, p. 268.

Stegodon insignis, KOKEN, 1885, Palaeont. Abhandl., vol. 3, pp. 14-16 [42-44], pl. 11, fig. 8.

Elephas insignis, LYDEKKER, 1886, Catalogue of fossil Mammalia in the British Museum, vol. 4, pp. 89, 97.

Stegodon insignis, SCHLOSSER, 1903, Abhandl. Bayerischen Akad. Wiss., vol. 22, pp. 44-45, pl. 14, fig. 10.

Stegodon orientalis grangeri OSBORN, 1929, Amer. Mus. Novitates, no. 393, pp. 16-17.

COTYPES: B. M. Nos. 41926, 41927, two fragments of teeth.

Referred Specimens: A.M.N.H. Nos.

18454, left DM_4 ; 18455, right and left DM^3 , mandible with right and left DM_3 , also right and left DM_3 , unattached, fragment of a DM_3 ; 18456, right DM_4 ; 18459, right DM^3 ; 18461, tooth fragments; 18536, right M^1 ; 18544, right DM^2 ; 18558, right DM^3 , fragments of rami with right and left DM_3 , fragment of a right DM_3 , left DM_4 ; 18578, fragment of right ramus with DM_3 , miscellaneous teeth; 18621, tooth; 18629, palate with right and left M^3 ; 18630, skull with right and left M^{1-2} ; 18630a, maxilla with right DM^4 (or M^1), left mandibular ramus with DM_4 , left mandibular ramus with M_1 ; 18631, left mandibular ramus with DM_4 , M_1 , also right and left DM_4 ; 18632, skull of a young animal with DM^{2-3} ; 18633, mandible, with right and left M_1 and right M_2 ; 18634, fragments of left M^2 or M^3 , and left M_2 or M_3 ; 18635, left mandibular ramus with DM_4 , unerupted; 18636, left DM^4 , jaws; 18637, left M_2 , also tooth fragments; 18638, skull of a young animal with DM_{2-3} supposedly associated with 18640 and 18641, left and right mandibles; 18642, mandible with left M_1 and right and left M_2 , right M_1 , also tooth fragments; 18643, left DM^3 , left maxilla with DM^{2-3} , also tooth fragments; 18644, left mandibular ramus with symphysis and DM_{2-3} , also tooth fragments; 18645, left DM_4 ; 18702, skull and mandible with right and left DM^{3-4} , DM_{3-4} ; 18703, palate and fragment of cranium of a young individual with right and left DM_{2-3} , DM_4 , unerupted, left mandibular ramus with symphysis and DM_{2-3} , DM_4 , unerupted; 18704, right mandibular ramus with M_{1-2} , also right DM^4 and left DM_4 ; 18705, right maxilla with DM^{2-3} , mandible with right and left DM_{2-3} ; 18707, fragment of right maxilla with DM^3 , mandibular rami with right and left DM_3 ; 18708, skull and jaw of an adult individual with right and left M^3 , M_3 ; 18709, left maxilla with DM^{2-3} , left mandibular ramus with DM_3 ; 18710, mandible with right and left DM_4 , M_1 , partially erupted; 18711, palate with right and left DM^{3-4} , mandible with right and left DM_{3-4} ; 18713, tusk; 18714, left M^3 , right and left M_3 . A.M.N.H. No. 18714 is the type of *Stegodon orientalis grangeri* Osborn.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: "A *Stegodon* which resembles

S. insignis Falconer and Cautley, but differs from it in having the ridges more widely spaced, in the lesser development of the cement and, in the greater lateral curvature of the lower molars, as well as the greater convexity of the occlusal surface of the upper molars" (Hopwood, 1935, p. 77).

DISCUSSION

The proboscidean material collected by Granger at Yenchingkou is here considered as belonging to the species *Stegodon orientalis* Owen, and Osborn's name *Stegodon orientalis grangeri* is regarded as synonymous with the older designation. There are several reasons for taking this action.

In the first place, upon *a priori* considerations it seems quite unlikely that there should be any specific or subspecific difference between the fossils originally described by Owen and those subsequently described by Osborn. Owen says that his type specimens came "from a cave, near the city of Chungking-foo, in the province of Sze-Chuen." Chungking is about 120 miles or so from Yenchingkou, and, like the other cities along this portion of the Yangtze, is enclosed by, or not far from, the great limestone ridges that parallel the river. In view of the fact that the fossils described by Owen are of the characteristic "drug-store" type and that mining operations for fossil bones have been long established on these ridges, there is every reason to believe that Owen's material and the fossils collected by Granger represent portions of the same fauna, possibly and very probably collected within the same general region on top of the limestone ridges. Consequently specific identities should be expected in a comparison of the two suites of fossils.

But aside from these considerations, which in this case are very important, there are the fossils themselves. Are the proboscideans studied by Osborn truly separable from the type material?

Osborn defined *Stegodon orientalis grangeri* as follows: "The subspecies *Stegodon orientalis grangeri* is more primitive than the type of *S. orientalis*, which is also from a cave in Sze-chuan; the ridge-crests are less elevated and wider apart at the base and seem to be even more primitive than those of the *S. insignis* type; the cranium is much smaller

and simpler than that of *S. insignis-ganesa* and resembles in its contour rather that of *S. bombifrons*" (Osborn, 1929, p. 17).

It is difficult to know from the type description exactly what differences were intended to be drawn between *Stegodon orientalis grangeri* and *Stegodon orientalis*. Certainly it is stated that the first-mentioned of these forms is more primitive than the latter; the only other differences are at most the less elevated and more widely spaced ridge crests of *S. orientalis grangeri* as compared with *S. orientalis*. If it be assumed that these were the differentiations intended, it is difficult on the basis of a comparison of the type figures and description with the descriptions and figures of referred specimens made by Koken, Schlosser, and Matsumoto and with the material collected by Granger to find any appreciable distinctions between them. In other words, there is no true basis for stating that the ridge crests in *Stegodon orientalis grangeri* are more primitive, i.e., lower and more widely spaced, than in *Stegodon orientalis*, as is evident from the measurements in table 29. In fact, all the characters supposedly differentiating *Stegodon orientalis grangeri* from *Stegodon orientalis* have a range of variability in measurements that includes the measurements for the type and referred specimens of *Stegodon orientalis*.

The specimens of *Stegodon orientalis* collected by Granger at Yenchingkou probably represent the best-known series in existence showing the growth stages in a fossil proboscidean, and it is safe to say that this series compares favorably with any extant sequence of recent proboscideans showing in a similar manner the growth from a very young individual to a fully adult animal. Consequently these fossils from Yenchingkou present an unusual opportunity for the study of changes accompanying growth in the Proboscidea, especially as they affect the skull, jaw, and teeth. These changes, as shown in the present series of *Stegodon orientalis*, were discussed to some extent by Osborn in the second volume of his great monograph of the Proboscidea.

The dentition offers the best opportunity in this study of growth within a single species, so that particular attention is paid to the changes in tooth form and dimensions from juvenile to adult in *Stegodon orientalis*.

TABLE 29
MEASUREMENTS (IN MILLIMETERS) OF TEETH OF *Stegodon orientalis*

A.M.N.H. Nos.	Tooth	L×W	Height, Penulti- mate Ridge Crest, Unworn	No. of Lamel- lae	Tooth	L×W	Height, Penulti- mate Ridge Crest, Unworn	No. of Lamel- lae	Depth of Ramus, Ante- rior End of Den- tition
18544	DM ²	24×26	12	3+	—	—	—	—	—
18455	DM ³	60×39	—	5+	DM ₃	60×36	21	6	52
18455	—	—	—	—	DM ₃	64×40	23	6	—
18558	—	—	—	—	DM ₃	50×32	—	5	—
18459	—	—	—	—	DM ₃	68e×40	26	6	—
18578	—	—	—	—	DM ₃	72e×42	28	6	46
18632	DM ²	20×19	—	3	—	—	—	—	—
18632	DM ³	44×33	—	5	—	—	—	—	—
18643	DM ³	52×35	18	5+	DM ₂	13×11	—	2?	—
18644	—	—	—	—	DM ₃	55×34	20	5+	73
18638 { (skull)	DM ²	20×20	—	3	DM ₂	13×12	—	2	65
18640 { (jaw)	DM ³	58×40	18	5+	DM ₃	62×33	17	6	—
18703	DM ²	25×26	—	3	DM ₂	16×16	—	2	84
18703	DM ³	61×41	22	5+	DM ₃	65×43	—	5+	—
18703	DM ⁴	115×60	35	6+	—	—	—	—	—
18705	DM ²	25×23	—	3	DM ₂	15×13	—	2	74
18705	DM ³	68×40	22	6	DM ₃	65×38	24	6	—
18707	DM ³	56e×36	16	5+	DM ₃	61×37	20	6	57
18709	DM ²	22×21	11	2+	—	—	—	—	—
18709	DM ³	63×43	23	5+	DM ₃	67×41	23	6	—
18702	DM ³	54×40	—	5+	DM ₃	54×38	—	—	78
18702	DM ⁴	97×53	26	6+	DM ₄	48	—	6a	—
18711	DM ³	60×41	—	5+	DM ₃	64×39	—	5+	110
18711	DM ⁴	108×59	28	7+	DM ₄	113×56	31	7+	—
18704	DM ⁴	108×60	29	7	DM ₄	126×58	33	7+	—
18558	—	—	—	—	DM ₄	117×57	31	7	—
18630a	DM ⁴	122×64	30	7+	DM ₄	130×62	33	7	105e
18636	DM ⁴	125×66	26+	7	—	—	—	—	—
18630	M ¹	(worn)	—	6a	—	—	—	—	—
18630	M ²	185×88	45	8	—	—	—	—	—
18536	M ^{1a}	182×89	45	7	—	—	—	—	—
18631	—	—	—	—	M ₁	215e×67	40	7+	155
18710	—	—	—	—	M ₁	—×65	42	7+	143
18637	—	—	—	—	M ₂	210×68	—	9	—
18704	—	—	—	—	DM ₄	125×57	32	7	130
18704	—	—	—	—	M ₁	171×74	42	8	—
18630a	—	—	—	—	M ₁	185×83	—	8	115
18708	M ³	105	55	12	M ₃	220+×90	45	8+	190
18633	—	—	—	—	M ₁	175×84	40a	7	170
18633	—	—	—	—	M ₂	220×95	53	9	—
18642	—	—	—	—	M ₂	197×74	48	8+	180
18629	M ³	225+×108	—	8+	—	—	—	—	—
18714	M ³	286×—	54	12	M ₃	360×—	55a	13	—
18643	DM ²	23×20	—	3	—	—	—	—	—
18643	DM ³	64×38	—	6	—	—	—	—	—

* Possibly M².

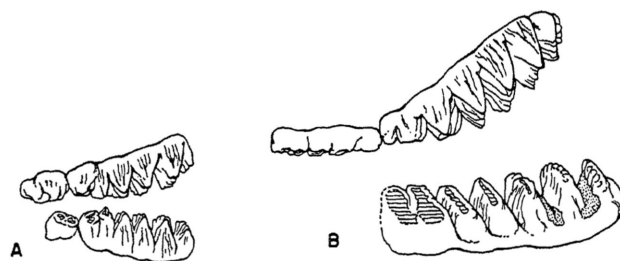


FIG. 27. *Stegodon orientalis* Owen. A. A.M.N.H. No. 18705, upper and lower left DM2-3 (right DM³ reversed). B. A.M.N.H. No. 18711, left DM³⁻⁴ and A.M.N.H. No. 18630a, left DM₄. Lateral views. One-fourth natural size. From Osborn (1942, fig. 759).

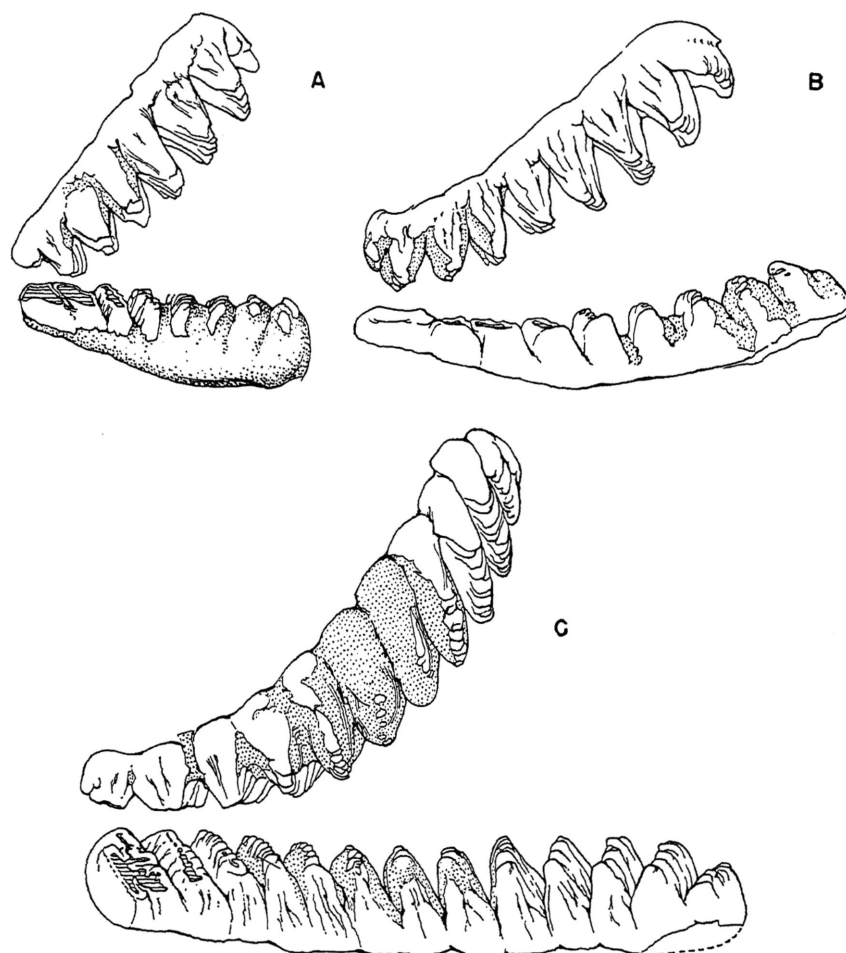


FIG. 28. *Stegodon orientalis* Owen. A. A.M.N.H. No. 18635b, upper and lower left M1 (M₁ reversed). B. A.M.N.H. No. 18642, upper and lower left M2 (M₂ reversed). C. A.M.N.H. No. 18714, upper and lower left M3. Lateral views. One-fourth natural size. From Osborn (1942, fig. 759).

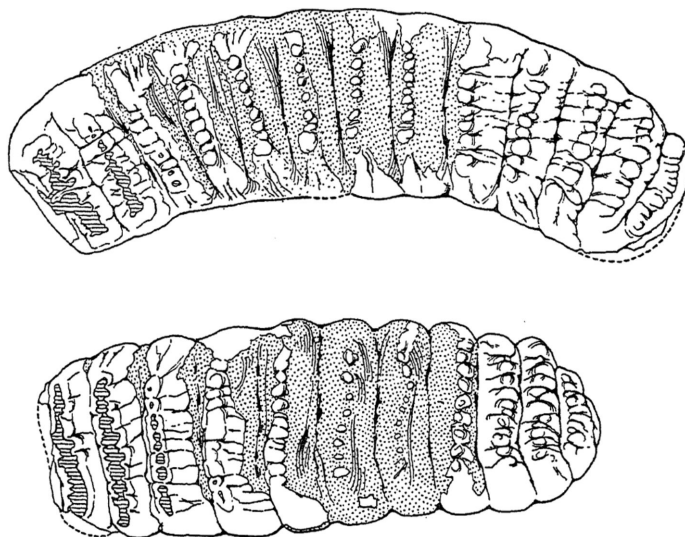


FIG. 29. *Stegodon orientalis* Owen. A.M.N.H. No. 18714, upper and lower left M3. Crown views. One-fourth natural size. From Osborn (1942, fig. 759).

Osborn gave the ridge-crest formulas for the six cheek teeth in *Stegodon orientalis* in a very exact manner, as shown below. After a careful study of all the material on hand representing the species under consideration, we feel that the ridge-crest formulas cannot be expressed with the exactitude indicated by Osborn. Accordingly these formulas as determined by the present authors and contained in table 29 are here compared with his:

OSBORN		THIS PAPER	
DP2	$\frac{1/2-2-1/2}{2}$	DM2	$\frac{3}{2}$
DP3	$\frac{5-1/2}{+5-1/2}$	DM3	$\frac{5-6}{5-6}$
DP4	$\frac{3/4-6-1/2}{7-1/3}$	DM4	$\frac{6-7}{7}$
M1	$\frac{1/3-6-1/2}{8}$	M1	$\frac{7}{7-8}$
M2	$\frac{1/3-8-1/3}{?9-1/3}$	M2	$\frac{8}{9}$
M3	$\frac{1/8-11-1/8}{1/2-13}$	M3	$\frac{12}{13}$

In these formulas precisely those teeth in which the greatest number of specimens are known show the greatest amount of variability. Thus in the third milk molar, the

most abundantly represented tooth of the series, there is a variability of one crest in a tooth having a maximum of six crests. It is felt that if more specimens were known of the true molars, a corresponding variability might also be found in these teeth. This is indicated to some degree by the variability in the first lower molar of one crest in a maximum of eight.

It is difficult to know just how to count the ridge crests in all cases. Small or incipient crests at the front or the back of the tooth lead to complications in deciding upon the exact number of crests in any single tooth, and it was the presence of these small crests that led Osborn to adopt his fractional indications, which were carried to rather an extreme. In the present study, such crests, if small, were disregarded; if large, they were given the status of a full crest.

For instance, in the third upper milk molar, a few teeth had only five crests, while a few had six. By far the greatest number of the teeth had five crests, with a fractional crest at the posterior end of the tooth, so it might be said that these teeth had five and a half or five-plus ridge crests. The ridge-crest formula for this tooth is thereby 5-6, with the median and the mode for the ridge crests at $5\frac{1}{2}$ or 5+. In the lower third milk molar the

LAMELLAE



FIG. 30. Graph showing increase in lamellar frequency in *Stegodon orientalis* Owen.

ridge-crest formula likewise is 5-6, but whereas the median is $5\frac{1}{2}$, the mode in this case is 6.

The progressive increase in the number of ridge crests per tooth is shown graphically in figure 30. The curve of the graph is drawn to points representing selected medians for each variable. The upper and lower dentitions are shown separately.

It is interesting, at this point, to show also the increase in lamellae during growth in *Stegodon orientalis* compared with such increases in *Elephas maximus* and in *Loxodonta africana*. The ridge-crest or plate formulas

for the two living forms are given by most authorities as follows: *Elephas maximus*, DM2-4, DM3-8, DM4-12, M1-12, M2-16, M3-24; *Loxodonta africana*, DM2-3, DM3-6, DM4-7, M1-7, M2-8, M3-10.

A comparable formula for *Stegodon orientalis*, with the medians of the variables and the averages between the upper and lower dentitions, would be about as follows: *Stegodon orientalis* DM2- $2\frac{1}{2}$, DM3- $5\frac{1}{2}$, DM4-7, M1-7, M2- $8\frac{1}{2}$, M3- $12\frac{1}{2}$.

If the number of ridge crests in M3 be represented by the number 100, the increase

in the ridge-crest formula from the second milk molar to the last molar can be shown by the tabulation on this page.

From this it is evident that in the increase of the ridge crests *Stegodon orientalis* resembles the Indian elephant somewhat more closely than it does the African form.

As might be expected, a curve similar to that for the ridge-crest increase is obtained when the actual lengths of the teeth are plotted. This has been done for the Szechwan form, using for the lengths the arithmetic means for the teeth in the series from the second milk molar to the last molar. The curves, one for the upper dentition and one for the lower, are shown in figure 31.

<i>Stegodon orientalis</i>	2½	5½	7	7	8½	12½
	20	44	56	56	86	100
<i>Elephas maximus</i>	4	8	12	12	16	24
	16.6	33.3	50	50	66.6	100
<i>Loxodonta africana</i>	3	6	7	7	8	10
	30	60	70	70	80	100

It is interesting to compare this chart with the previous one, particularly to point out a significant difference between them due to the manner in which the teeth develop in *Stegodon orientalis*. It will be noticed in the graphs showing the increase of the ridge crests during growth that there is a rather steady increase from the second milk molar to the fourth milk molar. Then the curve flattens out between this latter tooth and the first molar, to continue its upward trend from the first molar to the third molar, because, of course, the ridge-crest formula for the first molar repeats that for the last milk molar.

On the other hand, in the graphs showing the increase in length of the teeth from the second milk molar to the last molar there is likewise a steady increase, interrupted from a second upward trend by a break or a flattening of the curve. But in this case the break is between the first and second molars and is due to the fact that these teeth, although differing in ridge-crest formulas, are similar in size. This means, of course, that the individual ridge crests increase steadily in size to and including the first molar, that there is a drop in the individual ridge-crest size between the first and second molar, followed

again by an increase between the second and last molars.

The changes in the skull and jaw due to growth are known in a general way for the modern elephants and were outlined by Osborn in his monograph. As he pointed out, the Proboscidea follow the biogenetic law in that the skulls of very young individuals in most of the phylogenetic branches of the order show a marked similarity to one another. During the ontogenetic development, from infant to adult, the disparities characteristic of the various proboscidean genera become apparent.

Four stages in the growth of *Stegodon orientalis*, namely, the young animal, the

juvenile, the young adult, and the fully mature animal, were used in an attempt to determine the general trends in the ontogenetic development of this species.

The skull of a very young *Stegodon orientalis* resembles, as would be expected, the young skull in other types of proboscideans. It is relatively low and relatively long compared with the adult skull. The cranial portion of the skull is to a slight degree more posteriorly located with regard to the facial region than in the adult *Stegodon*, a feature in the young animal that is reminiscent, even though but slightly, of the typically mammalian condition. The nasal passage, although characteristically proboscidean, with the anterior aperture dorsal in position as compared with the posterior opening, is nevertheless more nearly horizontal in the young *Stegodon* than it is in the adult. The palate and the cheek teeth are not so much depressed with relation to the occipital condyle as in the adult *Stegodon*, and concomitantly the mandibular condyle is less elevated with regard to the occlusal surface of the lower cheek teeth in the young animal than in the adult. In addition, it seems that the tusk in the young *Stegodon* protrudes more

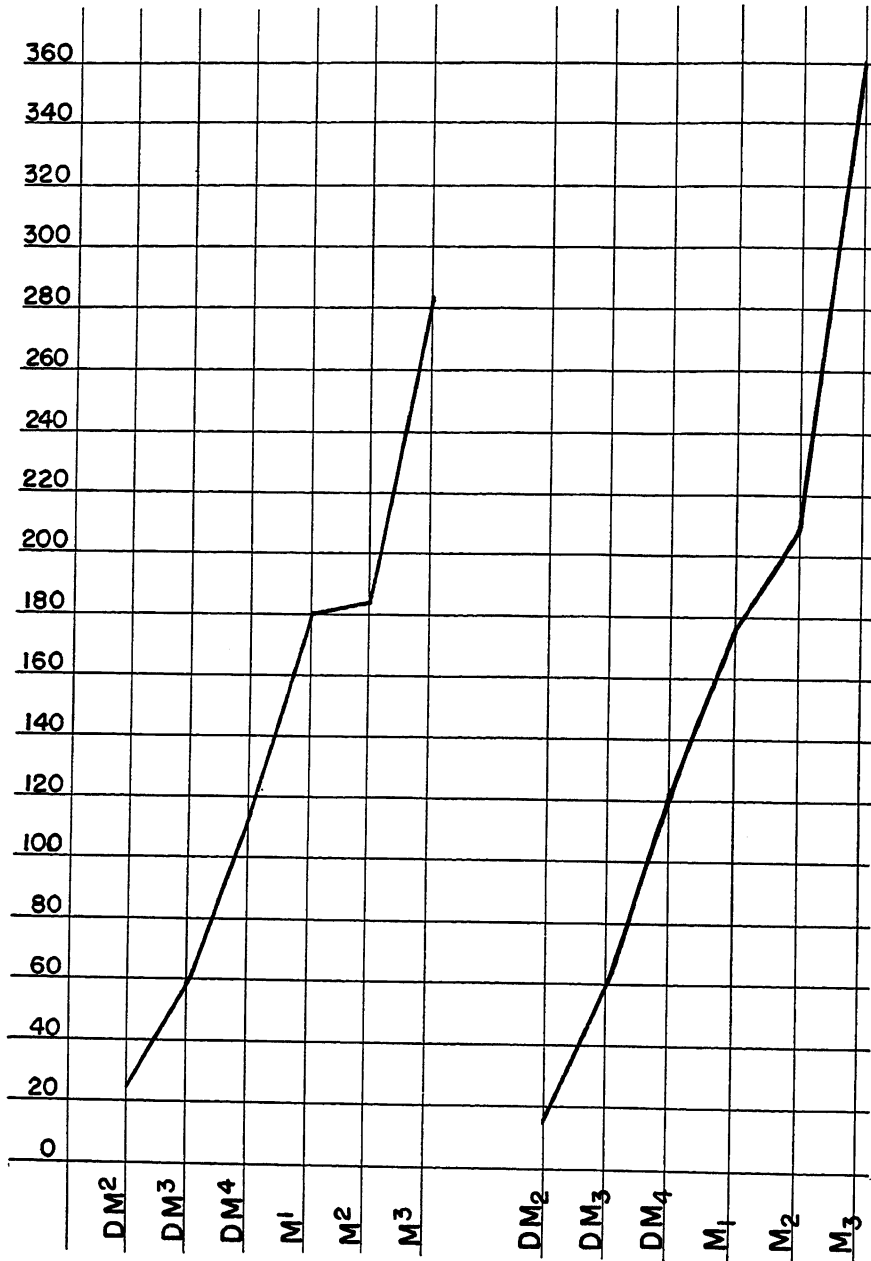


FIG. 31. Graph showing increase in tooth length in *Stegodon orientalis* Owen.

horizontally than in the adult, where of course it is directed strongly downward.

These changes involved in the growth from young to adult can be outlined somewhat as follows:

1. There is a deepening of the skull, which of course implies its relative shortening. This

deepening, or the progression of bathycephaly, is accomplished by the development of sinuses in the frontal portion of the cranium above the brain and in the palatal portion of the maxilla below the brain. Consequently the increase in the depth of the skull is differential, marked by a heightening of the

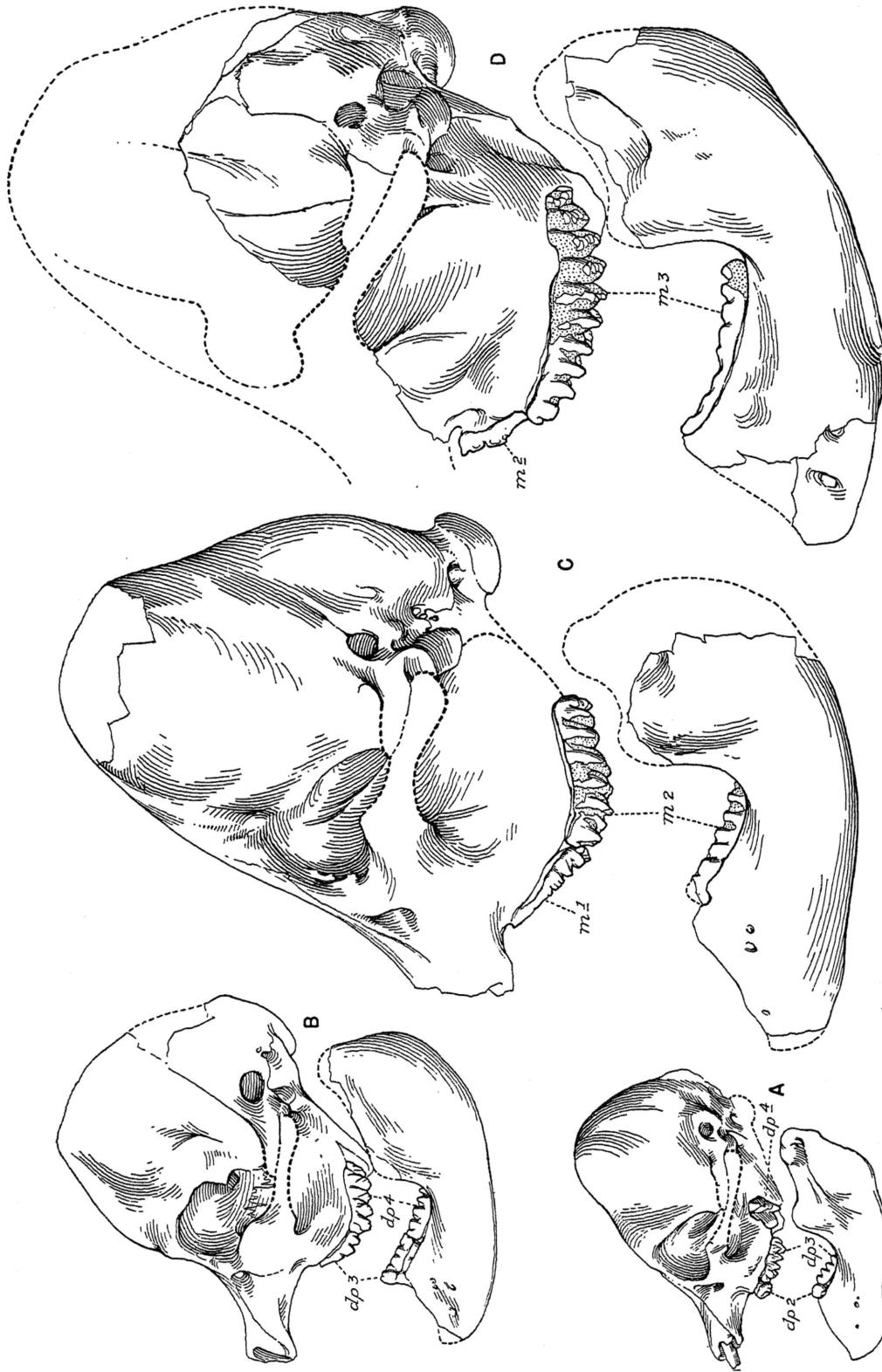


FIG. 32. *Stegodon orientalis* Owen. A. Infantile skull, A.M.N.H. No. 18638, and mandible, A.M.N.H. Nos. 18705, 18640. B. Juvenile skull, A.M.N.H. No. 18702, and mandible, A.M.N.H. No. 18711. C. Young adult skull, A.M.N.H. No. 18630, and mandible, A.M.N.H. No. 18636. D. Mature adult skull, A.M.N.H. No. 18708, and mandible, A.M.N.H. No. 18629. Left lateral views. One-eighth natural size. From Osborn (1942, fig. 763).

skull roof above the orbit and by a deepening of the maxillae below the zygomatic arch.

2. The upward growth of the top of the skull and the downward growth of the basal region result in the carrying dorsally of the anterior nasal choana and ventrally of the posterior choana. Therefore the nasal passage becomes more nearly vertical as the animal grows from the young stages into the adult condition.

3. With the upward growth of the cranium above the brain, there is a certain amount of pushing forward, so that the brain case and

its attendant sinuses come to occupy a position more nearly above the cheek teeth than is the case in the young animal.

4. Naturally, with the deepening of the basal region of the skull, the teeth are carried down in relation to the occipital condyles, and likewise in the mandible the condyle is carried up in relation to the occlusal surface. This is correlative in the more advanced proboscideans with the development of very tall cheek teeth, but that such tall teeth are not the sole factor involved in this change of proportion is shown by the fact that the

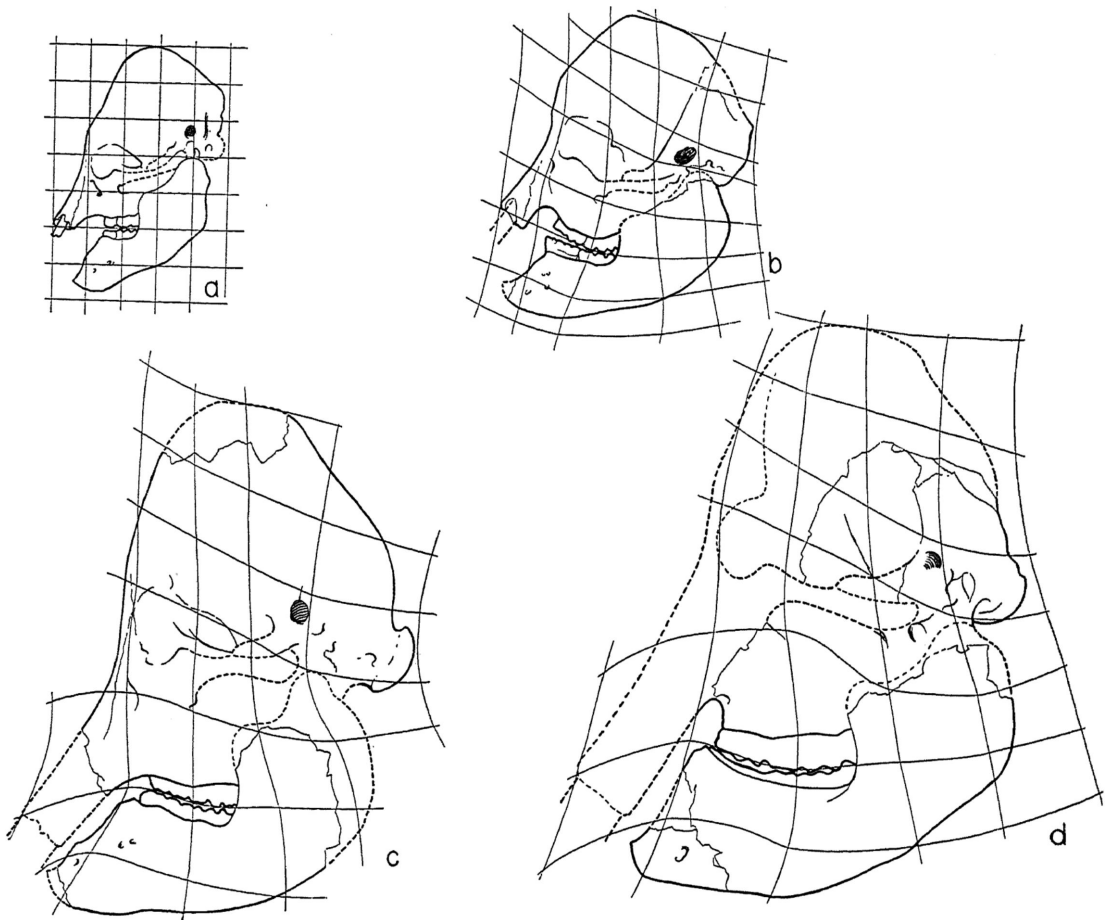


FIG. 33. Diagram showing by deformed coordinates changes in skull of *Stegodon orientalis* from very young to mature adult stage. A. Infantile skull, A.M.N.H. No. 18638, and mandible, A.M.N.H. No. 18705. B. Juvenile skull, A.M.N.H. No. 18702, and mandible, A.M.N.H. No. 18711. C. Young adult skull, A.M.N.H. No. 18630, and mandible, A.M.N.H. No. 18636. D. Mature adult skull, A.M.N.H. No. 18708, and mandible, A.M.N.H. No. 18629. Lateral views, all one-eighth natural size. A regular grid is superimposed upon the lateral view of the infantile skull. The points of intersection in this grid are located on the views of the other skulls and are connected by lines. The resulting deformation of the coordinates shows the differential changes in the skull during growth.

modification is quite marked in *Stegodon*, even though the cheek teeth are relatively low crowned.

5. There is seemingly a rotation of the alveolus for the tusk, as already mentioned, correlated with the more downwardly directed incisor in the adult, as compared with the young animal.

6. In a transverse direction there is a relative broadening of the skull in the growth from young to adult. This is apparent in the width of the skull compared with its height and, as Osborn has shown, in the development of certain individual bones, such as the nasals, which in the young are short and narrow while in the adult they are truncated and very broad.

These changes in proportion during growth are shown in figure 32.

To present the subject more graphically, the proportional changes due to growth are further illustrated in figure 33 by deformed coordinates, following the method first utilized by d'Arcy Thompson and modified by one of the present authors (Colbert, 1935, 1941; see also Simpson and Roe, 1939). In this figure, a series of regular coordinates are placed against the lateral view of the young skull in *Stegodon orientalis*. By the location on the skulls of successively older individuals of the intersections of the horizontal and vertical lines of the coordinates in approximately the same positions they occupy on the young skull, a series of deformed grids are constructed which show by their deformation the growth changes involved in the passage from young to adult animal. Thus it can be seen at once that the deepening of the skull is due to an upward growth above the orbital level and a downward growth below the orbit, that the difference in the shape of the young and the adult mandibles is due to an increase in length and a differential increase of the angular region, that there has been a downward growth of the incisor alveoli, and so on.

ELEPHANTIDAE

PALAEOLOXODON MATSUMOTO

Palaeoloxodon MATSUMOTO, 1924, Jour. Geol. Soc. Tokyo, vol. 31, pp. 257-272.

GENERIC TYPE: *Elephas namadicus naumanni* Makiyama.

DIAGNOSIS: A large elephantine with divergent tusks, and a very strong frontal crest due to a forward overgrowth of the frontal bones. Cheek teeth hypsodont, with wrinkled enamel. Loxodont sinus rudimentary or absent. About 18 to 20 ridge plates in the third molars.

Palaeoloxodon namadicus (Falconer and Cautley)

Elephas namadicus FALCONER AND CAUTLEY, 1846-1847, Fauna antiqua Sivalensis, pls. 12A-D, 13.

Elephas cf. *namadicus*, YOUNG, 1939, Bull. Geol. Soc. China, vol. 19, p. 328, figs. 5, 6.

Loxodonta (Palaeoloxodon) namadicus, MATSUMOTO, 1924, Jour. Geol. Soc. Tokyo, vol. 31, p. 269.

Palaeoloxodon namadicus, OSBORN, 1931, Amer. Mus. Novitates, no. 460, p. 20.

This elephant is not represented in the Yenchingkou collection made by Granger, but it should be included in the fauna on the basis of Young's records of a broken skull of a juvenile with milk teeth obtained at Yenchingkou by L. P. Chia in 1936.

PERISSODACTYLA

CHALICOTHERIIDAE

NESTORITHERIUM Kaup

Nestoritherium KAUP, 1859, Beitrage naheren Kenntniss urweltlichen Säugethiere, no. 4, p. 3.

GENERIC TYPE: *Chalicotherium sivalensis* Falconer and Cautley.

DIAGNOSIS: A brachyodont chalicothere, somewhat smaller than the genus *Chalicotherium*. Protoloph reduced or absent, while the anterior crest on the upper premolars is likewise absent. Protoselenid of lower cheek teeth well developed.

Nestoritherium sinense (Owen)

Chalicotherium sinense OWEN, 1870, Quart. Jour. Geol. Soc. London, vol. 26, p. 429, pl. 29, figs. 7-10.

Chalicotherium sinense, MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 573.

Circotherium sinense, MATTHEW, 1929, Bull. Amer. Mus. Nat. Hist., vol. 56, p. 519.

Circotherium sinense, COLBERT, 1934, Bull. Amer. Mus. Nat. Hist., vol. 67, pp. 384-385.

TYPE: B.M. No. 41934, a third right upper molar.

REFERRED SPECIMEN: A.M.N.H. No. 18453, a left lower molar, probably M_3 .

HORIZON AND LOCALITY: Pleistocene; Yen-chingkou, Szechwan, China.

DIAGNOSIS: "Larger than *C. sivalense*, of about the same proportions, and with the protoloph entirely absent on the molars. Protocone more clearly round-conical than in *C. sivalense*" (Colbert, 1934, p. 384).

DISCUSSION

The single tooth A.M.N.H. No. 18453 is the only specimen representative of the chalicotheres in the Yen-chingkou collection and was described as follows: "It is rather large, being somewhat greater in size than the similar tooth in *C. sivalensis*. It is characterized by a heavy posterior cingulum, and especially by the great reduction of the metastylid. This latter feature is characteristic of the progressive members of the Macrotherini" (Colbert, 1934, p. 385). The measurements (in millimeters) are: length, 47; width, 24; height of metaconid, 22.

TAPIRIDAE

MEGATAPIRUS MATTHEW AND GRANGER

Megatapirus MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, p. 588.

GENERIC TYPE: *Tapirus* (*Megatapirus*) *augustus* Matthew and Granger.

DIAGNOSIS: A tapir unique because of its very large size.

Megatapirus augustus Matthew and Granger

Tapirus (*Megatapirus*) *augustus* MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 588-593.

TYPE: A.M.N.H. No. 18433, a skull, lacking the upper portion of the facial region, the zygomatic arches, and the premaxillae, and a jaw lacking the mandibular condyles and incisors. The cheek teeth are all present except for left P_2 and right P_{2-3} .

PARATYPES: A.M.N.H. Nos. 18428, a partial skull, with right P^1-M^3 , left P^2-M^3 , and associated mandible with symphysis, containing incisors and canines and right P_4-M_3 , left P_2-M_3 ; 18431, crushed skull and mandible of a young individual, the skull with right DM^{2-4} , left DM^{2-4} , and the mandible with right and left DM_{2-4} , also a left

M^1 , right M^3 , and left M_2 ; 18432, right maxilla with P^1-M^3 , and mandible with right P_2-M_3 , left P_4-M_3 .

REFERRED SPECIMENS: A.M.N.H. Nos. 18419, maxillary fragments with right DM^4-M^1 and unerupted P^4 , left DM^4-M^2 , mandible with right P_2, P_4, M_{1-3} , left P_2-M_3 , also a left radius and a cervical vertebra; 18420, a small left radius; 18421, skull and jaw fragments with right P^2-M^2 and right P_3-M_2 ; 18422, left DM^2 , left P^2 , left DM^4 , right P^4 , right P_{2-3} in fragment of ramus and left P_{2-4} in fragment of ramus, also a right calcaneum and a third metatarsal; 18423, right P^4 and right P_2 ; 18424, maxillary fragment with right P^{2-4} ; 18425, fragment of premaxilla with left I^3-C and maxillary fragment with right M^3 , fragment of ramus with right M_{1-3} ; 18426, premaxillae and mandibular symphysis with upper and lower incisors and canines, also two upper molars; 18429, fragment of left maxilla with P^{2-4} , mandibular ramus with left M_{2-3} , also left humerus, portions of left tibia, left astragalus, and calcaneum, left metatarsals III and IV, right navicular and right metacarpal II; 18430, maxillary fragments with right P^{3-4} and left P^{2-3} , two mandibular rami with left P_2-M_1 , and left P_2-M_1 ; 18435, right P^{3-4} , M^{2-3} , I_3 , right P_2-M_3 , left P_2, M_1 ; 18436, left M^{1-2} ; 18457, fragment of maxilla with left P^2 ; 18458, left P^2 and fragments of lower molars; 18460, several deciduous upper and lower cheek teeth; 18462, fragment of maxilla with right P^2-M^1 , also left lower canine; 18548, right and left DM^3 , right DM_2 ; 18683, partial mandible; 18748, a virtually perfect skull and mandible with complete upper and lower dentition, the third upper and lower molars in process of eruption; 18749, a fine skull and mandible with a complete upper and lower dentition; 18752, palate with right and left I^{1-3} , C , P^{1-3} , DM^4 , M^{1-2} , with M^2 in eruption; 18754, palate with premaxillae, right and left P^1-M^3 , with M^3 in eruption; mandible with canines, right P_2-M_3 (M_3 in eruption), and left P_2-M_3 ; 18755, palate with right DM^{2-4} , M^{1-2} , left I^3 , DM^{2-4} , M^{1-3} (M^3 in eruption); mandible with right P_{2-4} , left P_{2-4} , M_1 ; 18756, palate with left P^{2-3} , DM^4 , M^{1-2} (M^2 in eruption); mandible with right and left P_{2-3} , DM_4 , M_{1-2} (M_2 in eruption). C.N.H.M. Nos. P.14158, right and

left mandibular ramus, associated, with DM_{2-4} , M_1 ; P.14159, right mandibular ramus with P_2-M_3 ; P.14155,¹ fragment of right maxilla with DM^{2-4} , M^1 (crowns of P^{2-4} and M^{2-3} are present but not erupted); P.14156, fragment of left maxilla with DM^{3-4} , M^1 (crowns of P^{3-4} present but unerupted); P.14157,¹ fragment of left maxilla with DM^1 and part of DM^2 . U.C.M.P. No. 30039, skull and mandible, subadult with M^3 unerupted and DM^4 still in place; P_4 already erupted.

DIAGNOSIS: "Distinctive Characters.—Teeth and skull about one-fourth larger lineally than *T. indicus* or *terrestris* and almost as much exceeding *T. sinensis* in size. Anterior premolars more molariform than in *T. indicus*, the inner cusp and cingulum much more developed, especially in p^1 which in *T. augustus* is wider than long (?). Skull very short and deep, the vomer higher and thicker than in *T. indicus*, much more so than in *T. terrestris*" (Matthew and Granger, 1923, p. 588).

DISCUSSION

Fossil tapir teeth presumably from Szechwan were described by Owen (1870) and were referred to a new species, *Tapirus sinensis*. Subsequently, Koken (1885) referred some material found in Yunnan to this same species. In a study of fossil and prehistoric teeth of *Tapirus* from Java, Sumatra, and China made several years ago by one of us (Hooijer, 1947b) it was shown that the supposed differential characters of *Tapirus sinensis* as compared with the living Malay tapir do not exist; the Chinese teeth are identical specifically with those of *Tapirus indicus*.

Tapirus sinensis, a synonym of *T. indicus*, is not present in the Yenchingkou collection. The first specimens of the Szechwan tapir to be made known were described by Schlosser (1903, p. 72, pl. 3, figs. 13, 15). This material, undoubtedly drug-store fossils, came from Ichang on the Yangtze River, and although Schlosser referred the fossils to *Tapirus sinensis*, it is quite clear that they are much too large for the living form but correspond in size with *Megatapirus augustus*, as already remarked by Matthew and Granger (1923,

p. 588), Zdansky (1935, p. 14), and Hooijer (1947b, pp. 254, 290).

In 1918 a Swiss traveler, Paul von Rautenfeld, secured a partial, deformed skull of a large tapir together with some bones which were found at Yenchingkou at a depth of about 20 feet. The description of this specimen did not appear, however, until 1928 (von Rautenfeld, 1928). In this paper von Rautenfeld refers the skull to the species named by Matthew and Granger, which is certainly correct.

The present species has been recorded from the Hoshangtung cave in Yunnan by Bien and Chia (1938). The four teeth described by them certainly belong to *Megatapirus* and prove that this form extended from Szechwan into Yunnan. To the south the gigantic tapir must have extended into Indo-China, and possibly even Java. Certain large teeth from Lang Son, Tonkin, Indo-China, first recorded by Mansuy (1916, pl. 1, figs. 5–8), have been referred to *Megatapirus augustus* by Patte (1928). Recently, von Koenigswald (1940, p. 61) recorded a lower molar from the Middle Pleistocene Trinil fauna of Patjitan in Java as probably belonging to this species. If this reference is correct, it would be the first time that we find *Megatapirus* in association with *Tapirus indicus*; *Tapirus pandanicus* Dubois from the Pleistocene of Java is conspecific with the recent Malay tapir (Hooijer, 1947b, pp. 279–284).

Megatapirus is at once distinguished from all other tapirs by its very great size. As Matthew and Granger have said, it is about one-fourth larger lineally than the modern tapirs or than the Pleistocene *Tapirus sinensis*, yet this statement hardly gives a complete idea as to the degree by which *Megatapirus* exceeds in size those other tapirs with which it has been compared, for in its volume the Yenchingkou tapir creates the impression of being more than twice as large as the modern animal. This is in fact the case, since a comparison of the volume involves third powers of the linear dimensions.

In their general aspects the skulls of *Megatapirus* and *Tapirus* are much the same: that is, the Yenchingkou tapir shows, broadly speaking, a proportional enlargement of the modern oriental tapir skull. In this respect it might be said that the comparison of the ex-

¹ C.N.M.H. Nos. P.14155–P.14157 very probably belong to one individual.

TABLE 30

MEASUREMENTS (IN MILLIMETERS) OF THE SKULL OF *Megatapirus*
augustus AND *Tapirus indicus*

	<i>M. augustus</i>				<i>T. indicus</i>	
	A.M.N.H. No. 18433	A.M.N.H. No. 18431	A.M.N.H. No. 18748	A.M.N.H. No. 18749	A.M.N.H.(M.) No. 14106	A.M.N.H.(M.) No. 1799
Skull, length pre-maxilla-condyle	—	410e	544	519	412	426
Preorbital length	—	170	251	245	185	194
Postorbital length	295	240e	293	274	227	232
Height at M ³	238	182	251	235	194	201
Cranium, length	—	—	215	210e	204	211
Nasals, length	—	—	122	130e	119	116
Zygomatic width	—	—	267	240e	197	209
Postorbital constriction, width	—	—	81	83	85	81
Upper premolar series, length	108	—	119	111	89	74e
Upper molar series, length	100	89a	100e	101	76e	71
Mandible, length	—	—	450	445	332	337
Lower premolar series, length	92e	—	97	91	76	66
Lower molar series, length	104	107a	111e	105	—	69

tinct type is certainly with *Tapirus indicus*, as might be expected, rather than with *Tapirus terrestris* or *Tapirella bairdii*. This is to be seen especially in the form of the sagittal crest, which in *Megatapirus* and the modern oriental tapir is double along the top of the rather expanded cranium, while in the American form it is high and sharp; in the development of the channels and pits for the nasal diverticula, absent in *Megatapirus* (undoubtedly a secondary loss), shallow in the oriental tapir, and deep in the American form; in the flanges on the maxillae which project upward to embrace the forward portion of the ossified nasal septum, features that are quite characteristic of the Old World tapirs and are missing in the American forms; and in certain details of the teeth. Yet in spite of these diagnostic resemblances which unite *Megatapirus* with *Tapirus indicus* and separate it from the American tapirs, certain differences can be seen between the fossil and recent Old World forms, which for the most part distinguish *Megatapirus* as an animal more specialized than any of the modern tapirs. These characters are discussed here on the basis of a

comparison between the fossil and recent oriental types.

One notable difference between the skulls of *Megatapirus* and *Tapirus* is the relatively short cranium of the extinct type compared with that of the persisting species. This difference may readily be seen by a comparison of the length from the tip of the frontals to the back of the occipital crest with the total length of the skull in the two forms. It is shown also by the fact that the anterior tip of the frontals is above the second molar in the fossil, whereas it is not quite so retracted in *Tapirus indicus*, being above the first molar. Again it is shown by the fact that this same point, the anterior border of the frontals, is considerably behind the orbit in *Megatapirus*, whereas it is more nearly above the orbit in the modern oriental tapir. Finally it is shown by the comparatively greater length of the diastema of *Megatapirus* than that of *Tapirus*.

The other differences between *Megatapirus* and *Tapirus* are those of detail. Correlative with the shortening of the cranium in *Megatapirus* are a retraction and reduction of the

nasals, as compared with those of the modern *Tapirus*. For instance, the tip of the nasals in the fossil is above the third premolar, whereas in the modern animal it is above the first premolar.

Not only are the nasal bones shorter in *Megatapirus* than in *Tapirus*, but they are also relatively less bulky. Thus in the fossil the nasals are much more attenuated in their anterior portion than in the modern tapir,

with the result that their lateral outlines are strongly concave, as compared with the rather straight lateral edges of the nasals in *Tapirus*. Another difference, already mentioned, is the virtual absence in *Megatapirus* of any pits or depressions in the postero-superior surface of the nasal bones—characters of great prominence in the modern *Tapirus*. There are very slight indications of these pits in the Yenchingkou fossil, it is

TABLE 31
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Megatapirus*
augustus AND *Tapirus indicus*

	<i>M. augustus</i>											<i>T. indicus</i> (Recent), Hooijer, 1947b	<i>T. i. intermedius</i> , Hooijer, 1947b
	A.M.N.H. No. 18433	A.M.N.H. No. 18749	A.M.N.H. No. 18748	A.M.N.H. No. 18428	A.M.N.H. No. 18424 ^a	A.M.N.H. No. 18432	A.M.N.H. No. 18754	A.M.N.H. No. 18752	A.M.N.H. No. 18462	C.N.H.M. Nos. P.14155, P.14156	U.C.M.P. No. 30039		
P ¹													
L	27	27	28	27	25	28 ^b	26	29	27	—	29	19-22	22-23
W	25	22	26	24	23	22 ^b	23	24	25	—	25	14-21	17-19
P ²													
L	28	29	31	27	29	—	29	32	30 ^c	31	31	22-24	24-26
Wa	30	29	32	28	31	—	30	30	30 ^c	29	35	17-23	22-24
Wp	32	32	36	34	35	34	34	35	36	36	40	24-27	28-29
P ³													
L	29	31	31	29	30	30	30	31	31	31a	31	22-25	24-27
Wa	37	37	39	37	38	37	38	36	36	—	41	26-29	29-33
Wp	36	36	39	38	38	38	37	39	37	37	42	26-28	29-32
P ⁴													
L	30	29	30	29	30	32	33	—	33	—	—	22-23	24-27
Wa	38	40	40	40	40	39	39	—	40	38	—	28-31	30-33
Wp	36	38	38	39	39	39	38	—	37	—	—	26-29	28-32
M ¹													
L	33	—	35	32	32	33	33	35	—	35	35	24-27	25-28
Wa	38	36	41	41	40	37	39	38	—	38	43	24-28	27-30
Wp	34	32	35	36	36	32	33	34	—	34	37	22-25	25-27
M ²													
L	36	36	37	37	37	34	37	—	—	—	38	25-28	28-32
Wa	41	41	42	44	44	39	42	—	—	—	46	29-31	31-34
Wp	37	36	38	39	39	36	37	—	—	—	40	24-28	26-30
M ³													
L	34	38	—	35	36	36	—	—	—	—	—	24-28	30
Wa	40	41	—	39	41	40	—	—	—	—	—	27-30	32
Wp	31	33	—	31	32	32	—	—	—	—	—	23-25	27

^a The measurements of P⁴-M³ in this column are from specimen A.M.N.H. No. 18428.

^b A.M.N.H. No. 18460.

^c A.M.N.H. No. 18457.

TABLE 32
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Megatapirus*
augustus AND *Tapirus indicus*

	<i>M. augustus</i>								<i>T. indicus</i> (Recent), Hooijer, 1947b	<i>T. i. intermedius</i> , Hooijer, 1947b
	A.M.N.H. No. 18433	A.M.N.H. No. 18749	A.M.N.H. No. 18748	A.M.N.H. No. 18428	A.M.N.H. No. 18432	A.M.N.H. No. 18754	C.N.H.M. No. P.14159	U.C.M.P. No. 30039		
<i>P</i> ₂										
L	—	33	35	—	36	33	35	34	25-28	27-30
W	—	20	22	20	20	20	20	20	13-17	16-20
<i>P</i> ₃										
L	30	29	32	31	32	29	33	30	23-27	27-29
W	22	21	23	23	22	22	21	22	15-18	18-20
Wp	23	23	25	24	24	24	24	24	17-20	21-23
<i>P</i> ₄										
L	32	30	32	31	32	32	30	32	23-25	26-29
Wa	25	25	25	25	26	25	24	25	18-20	20-22
Wp	25	24	26	24	25	26	25	26	19-22	22-24
<i>M</i> ₁										
L	—	—	34	32	34	34	34	33	24-27	27-31
Wa	25	25	26	25	26	25	24	25	17-20	19-23
Wp	23	23	26	23	23	24	25	23	17-19	19-20
<i>M</i> ₂										
L	36	35	38	36	36	37	36	39	26-28	30-34
Wa	27	29	27	27	27	27	26	28	20-22	23-24
Wp	25	25	25	26	25	26	25	26	18-21	22-23
<i>M</i> ₃										
L	38	39	—	37	40	—	38	—	24-29	32-34
Wa	28	29	—	28	28	—	27	—	19-21	24-25
Wp	24	24	—	25	24	—	24	—	18-19	22

true, but they are so slight as to be almost non-existent. In the modern tapirs these depressions on the upper surface of the nasal bones accommodate the posterior terminations of the large nasal diverticula, which are characteristic of and prominent in many perissodactyls. There is a sort of channel in the upper surfaces of the long maxillary-frontal junction in *Tapirus* within which rests the tube of the nasal diverticulum, and this channel leads to the above-mentioned depression, one in each nasal, in which the diverticulum finds its ending. In *Megatapirus* such a bony channel for the diverticulum is but slightly developed, and this, together with the minute size or absence of the pits in the nasals themselves, leads to the conclu-

sion that the diverticula in *Megatapirus* were relatively much smaller than in the modern tapir, a development that is certainly a secondary and specialized character.

Another very interesting feature in this region of the fossil skull is the tremendous expansion of the frontal bone in the post-orbital region to form a large, egg-shaped "bulla." Careful probing indicates that this bulbous expansion is quite hollow—a sort of large and local frontal sinus, the purpose of which is conjectural. This is in the region for the insertion of the maxillo-labialis superior muscle and also for the naso-labialis muscle, so there may be a correlation between this frontal enlargement and the possible development of enlarged muscles controlling the

upper lip. On the other hand, it is just as probable that the swelling of the frontal in the postorbital region of *Megatapirus* was a disharmonic accompaniment to the general increase in size in this animal.

As is so often the case in mammalian evolution, the increase in size of *Megatapirus* has resulted in a brain case relatively smaller than that of *Tapirus*. Correlative with this development is the relatively greater constriction of the postorbital region of the parietals in *Megatapirus* as compared with *Tapirus*.

Other minor differences between the two genera are the result of the attainment of great size by *Megatapirus*. Thus the crests on the top of the skull, particularly the lambdoidal crest, are generally heavier and more prominent in the fossil than in the recent

species. This may be correlated in part with the relatively heavier neck muscles in the gigantic Pleistocene animal, necessary for the support of the large skull. Also, the pterygoids are comparatively heavy in *Megatapirus*, for the origin of strong muscles. There might be noted in addition the fact that the postglenoid and paroccipital processes are either in contact or very close together in *Megatapirus*, thereby forming a closed or almost closed external auditory meatus, while in the modern tapir the ventral part of the meatus is very broadly open. However, this is apt to be a strongly variable character in any perissodactyl species and cannot be accorded much weight in a recital of distinctive characters for the Yenchingkou tapir.

Generally speaking, the teeth in the fossil form are a large edition of the teeth in *Ta-*

TABLE 33
MEASUREMENTS (IN MILLIMETERS) OF MILK TEETH OF *Megatapirus*
augustus AND *Tapirus indicus*

	A.M.N.H. No. 18431	<i>M. augustus</i> A.M.N.H. No. 18755	C.N.H.M. No. P.14155, P.14158	<i>T. indicus</i> (Recent) Hooijer, 1947b	<i>T. i. intermedius</i> , Hooijer, 1947b
DM ¹					
L	26	—	27	19–22	22–23
W	22	24	24	14–21	17–19
DM ²					
L	30	32	—	23–25	25–28
Wa	28	27	—	19–22	22–23
Wp	31	30	31a	22–25	24–26
DM ³					
L	32	31	33a	24–25	25–28
Wa	32	31	—	23–26	24–29
Wp	30	30	—	21–24	22–27
DM ⁴					
L	—	33 ^a	35	23–26	25–28
Wa	—	36 ^a	37	25–27	24–29
Wp	—	32 ^a	33	22–24	22–27
DM ₂					
L	39	39	41	27–32	31
W	21	21	23	13–16	18
DM ₃					
L	33	31	33	23–26	26–30
Wa	20	20	21	15–16	16–18
Wp	22	21	22	14–17	17–19
DM ₄					
L	35	33	35	24–27	26–29
Wa	23	22	23	16–18	18–20
Wp	24	23	23	15–18	17–20

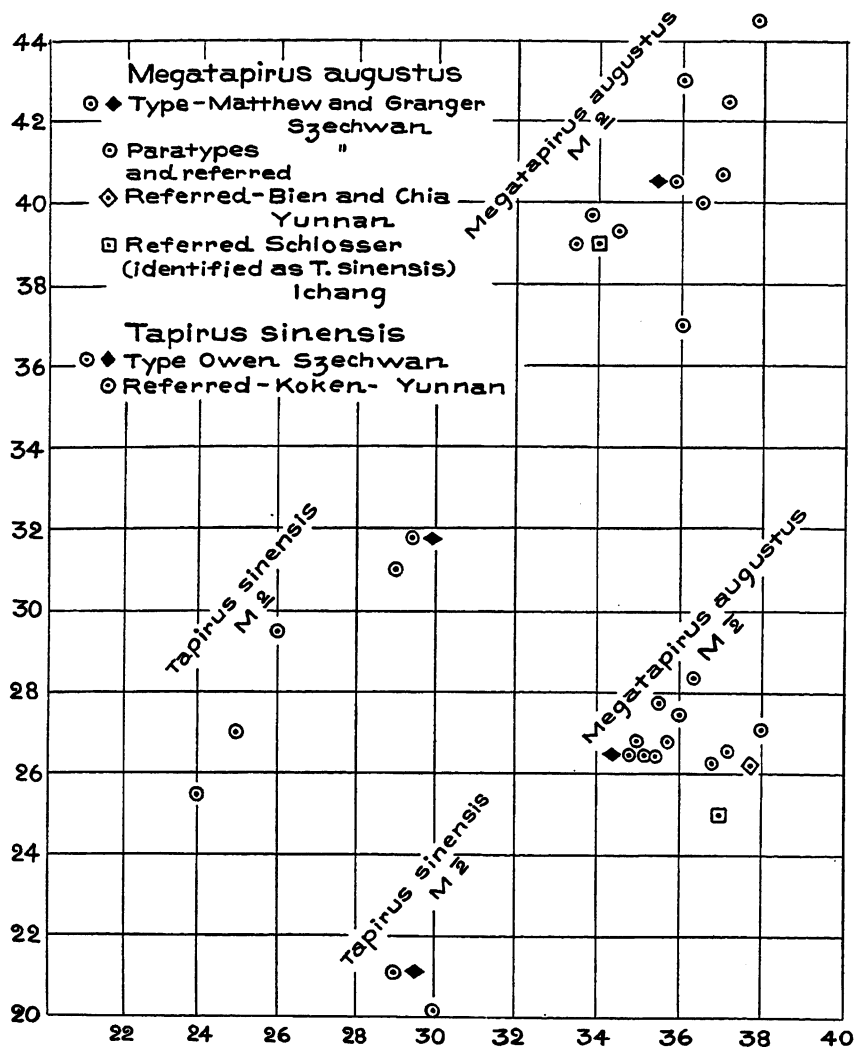


FIG. 34. Scatter diagram of corresponding lengths and widths of second upper molars in *Megatapirus augustus* and *Tapirus sinensis*.

pirus, but there are certain differences worthy of notice. In the first place, the cheek teeth of *Megatapirus* are characterized by relatively heavy anterior and posterior cingula, a point noted by Matthew and Granger. Also, as has already been pointed out by these authors, the anterior upper premolars are slightly more specialized in *Megatapirus* than in the modern tapir. Thus the first upper premolar is distinguished by the large size of its internal cusp, making the transverse diameter of the tooth almost equal to the antero-posterior diameter (Colbert, in Hooijer, 1947b, p. 292). However, there is a fair

amount of variation in the development of the inner cusp or hypocone in the first upper premolar in *Tapirus indicus*, and in one recent specimen (no. 17 in table 1, Hooijer, 1947b, p. 296) the transverse diameter (21 mm.) is only 1 mm. less than the antero-posterior diameter (22 mm.). On the other hand, some specimens of *Megatapirus* have a weak hypocone on P¹, making the width of the tooth decidedly less than the antero-posterior diameter (A.M.N.H. Nos. 18749, 18752, and 18460 in table 31), which is usual in *Tapirus indicus*.

In the second upper premolar of *Mega-*

tapirus there is a ridge descending outward and forward from the protocone which is continued to the base of the ectoloph, at the antero-internal side of the paracone. This anterior transverse crest, although variable in development, is more developed than in the Malay tapir, in which it is sometimes virtually absent and only the isolated protocone remains. In *Megatapirus*, furthermore, the antero-transverse diameter of P² is less different from the postero-transverse diameter than in most of the *Tapirus indicus* specimens, which are distinctly narrower in front than behind.

Consequently in the anterior upper premolars *Megatapirus* shows a certain advance over the living Malay tapir, although the difference is not very marked.

In addition to this, the upper molars of *Megatapirus* are wider than long to a greater extent than in *T. indicus*; the upper molars in the Yenchingkou tapir are relatively broader than those in the Malay tapir, both recent and subfossil. A prehistoric race of *Tapirus indicus* from limestone caves in central Sumatra, described by one of us (Hooijer, 1947b), has teeth that are larger than their homologues in recent Sumatran skulls but smaller than those of *Megatapirus*; it is truly intermediate in dimensions and almost completely fills the gap between recent *T. indicus* and *Megatapirus* as far as tooth size is concerned, with the exception of the widths of the upper molars in which there remains a hiatus (Hooijer, 1947b, p. 291). Incidentally, teeth of the same size as those from the prehistoric limestone caves of central Sumatra, *Tapirus indicus intermedius*, have recently been recorded from the Quaternary site of Houei Hoc, Haut-Laos, Indo-China, by Saurin (1950).

The succession of milk and permanent cheek teeth is shown by a series of upper and lower jaws. Several steps in the dental succession are distinguishable, as shown by the fossil material, and may be outlined in the following fashion:

1. In the very young animal the three milk molars are present, but at an early age the first permanent molar makes its appearance.

2. While the milk teeth are still in use the first permanent molar erupts, and the second

permanent molar appears in the alveolus.

3. As the second permanent molar comes into place the anterior premolars push out, to displace the first two milk molars. Thus the first, second, and third upper premolars and the second and third lower premolars come into position. The dentition now consists of a series of permanent teeth, but with one deciduous tooth, the fourth milk molar, still functioning.

4. Next the fourth milk molar is displaced by the erupting fourth permanent premolar, and at the same time the last permanent molar is coming into place.

5. Finally, the last molar erupts, and the dental succession is completed.

The process may be represented by the following formulas:

$$\begin{array}{rcl}
 & & M1 \\
 1. & \frac{DM2-DM3-DM4}{DM2-DM3-DM4} & \\
 & & M1 \\
 & & M2 \\
 & \begin{array}{cccc} P1 & P2 & P3 & P4 \end{array} & \\
 2. & \frac{DM2-DM3-DM4-M1}{DM2-DM3-DM4-M1} & \\
 & \begin{array}{ccc} P2 & P3 & P4 \end{array} & \\
 & & M2 \\
 & & M3 \\
 & \begin{array}{c} P4 \end{array} & \\
 3. & \frac{P1-P2-P3-DM4-M1-M2}{P2-P3-DM4-M1-M2} & \\
 & \begin{array}{c} P4 \end{array} & \\
 & & M3 \\
 & & M3 \\
 4. & \frac{P1-P2-P3-P4-M1-M2}{P2-P3-P4-M1-M2} & \\
 & & M3 \\
 5. & \frac{P1-P2-P3-P4-M1-M2-M3}{P2-P3-P4-M1-M2-M3} &
 \end{array}$$

The third upper incisor of *Megatapirus* is greatly enlarged and caniniform, and it occludes with the lower canine, which has shifted forward to occupy a position in the lower incisor series. Thus these two teeth function as canines, a condition typical of the modern *Tapirus*, but perhaps not quite so pronounced in the modern animal as in the fossil, owing to its smaller size and the

consequent lesser growth of individual parts. The upper canine in *Megatapirus* is relatively small and separated from the caniniform third incisor by a diastema.

There is little to be said about the postcranial skeleton in *Megatapirus*. Such bones as are preserved are similar to the same elements in *Tapirus* but are larger and heavier, as might be expected.

From the foregoing, it is apparent that *Megatapirus* might be said to represent the culmination of evolution in the tapirs, in that it is more specialized along those lines of adaptation that have characterized modern tapirid development than are any of the surviving forms. Although the specializations of *Megatapirus* over *Tapirus* are not large, they are nevertheless distinct and of such magnitude as to show the final trend of tapirid evolution.

In view of these considerations, what should be the generic position of the extinct tapir from Szechwan? Matthew and Granger regarded it as a subgenus of the genus *Tapirus*, and there is much to be said for this point of view. On the other hand, since distinct evolutionary trends are shown by the fossil over the recent form, and since it is a fact that the fossil is in certain respects more different from the recent tapirs than any of them are from one another, there is a good argument for regarding *Megatapirus* as a distinct genus. This latter viewpoint is adopted in the present work.

RHINOCEROTIDAE

RHINOCEROS LINNAEUS

Rhinoceros LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 56.

GENERIC TYPE: *Rhinoceros unicornis* Linnaeus.

DIAGNOSIS: Large rhinocerotids, with an elongate skull having a high occipital crest, and distinguished by a single dermal horn on the nose. Nasal bones arched. No post-orbital processes. Teeth moderately hypsodont.

Rhinoceros sinensis Owen

Rhinoceros sinensis OWEN, 1870, *Quart. Jour. Geol. Soc. London*, vol. 26, pp. 424-426, pl. 29, figs. 1-3.

Rhinoceros sinensis, KOKEN, 1885, *Palaeont. Abhandl.*, vol. 3, p. 52.

Rhinoceros sivalensis KOKEN, 1885, *ibid.*, p. 58 (in part).

Rhinoceros plicidens KOKEN, 1885, *ibid.*, p. 50.

Rhinoceros simplicidens KOKEN, 1885, *ibid.*, p. 60.

Rhinoceros sivalensis, LYDEKKER, 1886, *Catalogue of the fossil Mammalia in the British Museum*, pt. 3, p. 130, 131.

Rhinoceros sinensis, MATTHEW AND GRANGER, 1923, *Bull. Amer. Mus. Nat. Hist.*, vol. 48, pp. 567, 572-573, figs. 1, 2.

LECTOTYPE: B.M. No. 41935, third left upper molar, lacking the outer portion.

COTYPES: B.M. Nos. 41936, posterior portion of M¹; 41936a, ectoloph of left P⁴; 41941-41944, five lower cheek teeth.

REFERRED SPECIMENS: A.M.N.H. Nos. 18628, a crushed skull with left P²-M² and right DM¹, P²-M³ (this specimen was designated by Matthew and Granger as the neotype; also included under this number are various teeth, as follows: left DM³, right DM⁴, right M₂₋₃, left M₃, right P₂₋₃, left P₂₋₄, fragmentary right ramus with worn teeth, metapodials); 18470, right DM³ or DM⁴; 18471, left maxilla with DM⁴, M¹; 18486, right DM³, left DM⁴; 18511, fragmentary left ramus with cheek teeth; 18538, left lower cheek teeth; 18539, several lower cheek teeth; 18540, upper and lower incisors; 18547, right DM²; 18560, jaws; 18606, maxilla with right P²-M³, maxilla with left P³-M³; 18607, maxilla with right P²-M³, mandibular ramus with right P₂-M₃; 18609, fragment of an upper molar, right P₄, and a right femur; 18610, left maxilla with DM¹⁻⁴, M¹ in alveolus; 18611, fragmentary skull and jaw of a juvenile animal with right DM²⁻⁴ and right DM₂₋₄; 18612, right P⁴, M¹, M², left P³, DM⁴, M², M³, right ramus with DM₄, M₁₋₂ (in alveolus), metatarsal; 18613, right DM², DM³, DM⁴, P², DM₃, M₁ (?); 18614, patella; 18615, right P³ or P⁴, right lower cheek tooth, fragments of teeth; 18616, left P₃; 18617, right DM⁴, fragment of right DM⁴, left P₂, right astragalus; 18618, three lower molars; 18619, left P⁴, right DM₄, left lower cheek tooth; 18622, right P³⁻⁴, M¹, left M¹⁻³, right M₁₋₃; 18623, right M¹, mandible with right DM₂₋₄, M₁₋₂, left P₂₋₃ (in alveoli), DM₄, M₁₋₂, maxilla with left DM¹⁻³, mandible with left DM₂₋₄, mandible with right DM₄, left DM³⁻⁴, left

DM³, three right DM³, right DM³ or DM⁴, maxilla with two molar fragments, right lower cheek tooth, atlas, axis, two cervicals, five dorsals, calcaneum, 11 metapodials; 18625, palate with right and left DM¹⁻⁴, M¹⁻², P²⁻⁴ (in alveoli), mandible with right and left DM¹⁻⁴, M¹⁻², premolars and M³ (in alveoli); 18626, skull with right and left DM¹⁻⁴, M¹⁻², premolars and M³ (in alveoli), mandible with right and left DI, DM¹⁻⁴, M¹⁻², premolars and M³ (in alveoli); 18626a, right P⁴, M², left M¹, M², right lower molar; 18627, right ramus with M¹⁻³, left ramus with M³; 18758, maxilla with right DM¹⁻⁴, mandibular ramus with left DM¹⁻⁴, M¹ (in alveolus); 18780, right P², P⁴, DM⁴, M¹⁻³, left P², P³⁻⁴, DM⁴, M¹, fragmentary ramus with left P²⁻³, ramus with right P², ramus with right M¹⁻², various lower cheek teeth and incisors; 18781, right M², left DM³, left DM² in fragmentary ramus; 18782, right DM¹⁻³, right and left DM¹, ramus with left DM²⁻⁴, ramus with left DM⁴, M¹, ramus with left M¹ or M²; 18783, maxilla with left P^{3-M1}; 18784, left DM⁴, left M² or M³; 18785, right P⁴, left M³, right M³, fragment of upper molar; 18786, right P²; 18787, right P², three right lower cheek teeth; 21790, right lower molar. C.N.H.M. No. P.14160, right P^{2-M3} and left P^{3-M3}, associated. Also a right mandibular ramus with P^{2-M3}, and left M^{1-M3}, associated.

DIAGNOSIS: "Characters.—A large nasal horn. No clear indications of a second horn. Occiput apparently rather posterior in position. Teeth moderately hypsodont, slightly less so than in *R. indicus*. Premolars 130; length of molars, 160; p¹ small, deciduous. Both external ribs prominent on p²⁻⁴, posterior rib weak on m¹, wholly absent on m²⁻³, the anterior rib prominent on all three molars. Crochet prominent on p^{3-m3}, doubled on p^{4-m1}; crista rudimentary except on p², where it is prominent. No antecrochet save as an obscure swelling. Postfossette on p^{3-m1} only when considerably worn. The two inner cones of p² strongly twinned, slight twinning on p³⁻⁴" (Matthew and Granger, 1923, p. 572).

DISCUSSION

The relationships of *Rhinoceros sinensis* were ably discussed by Matthew and Granger

in 1923, and in the light of additional studies on the rhinoceroses from the Pleistocene of Szechwan there seems to be no reason for modifying the conclusions arrived at by those authors. However, it may be well to review the problem briefly.

Rhinoceros sinensis was described by Owen in 1870. Subsequent to Owen's original description of the species, various authors studied fossil rhinoceroses from China and came to diverse conclusions regarding their affinities. Koken, in 1885, recognized *Rhinoceros sinensis* among the materials he was studying from China, but in addition he also recognized *Rhinoceros sivalensis* and named two new species, *Rhinoceros simplicidens* and *Rhinoceros plicidens*, in the Chinese material at his disposal. This is an unnecessary complication of the matter, for comparison of Koken's plates with the large series of *Rhinoceros sinensis* teeth in the American Museum collection shows that without doubt all Koken's material belongs to the single species originally described by Owen. Koken was misled by the considerable variability in the dental characters of *Rhinoceros*, a subject elucidated at greater length below. The same is true of Schlosser, who recognized the several species designated by Koken and in addition designated another form, *Rhinoceros antiquitatus*, of probable Pleistocene age. These authors (working on mixed collections) between them also identified in the Chinese material *Rhinoceros brancoi*, *Aceratherium blanfordi*, *Aceratherium blanfordi hipparionum*, and *Aceratherium habereri*, forms of Pliocene age, the last three of which are now placed in the genus *Chilotherium*.

Lydekker in 1886 went to the other extreme by placing *Rhinoceros sinensis* in synonymy with *Rhinoceros sivalensis*. Finally Matsumoto in 1915, working with material from the Szechwan fissures but supposing he had two distinct faunas of different age, identified the rhinoceroses in his collection as *Aceratherium blanfordi hipparionum*, *Rhinoceros sinensis*, and *Rhinoceros plicidens*.

The solution of the problem, based on a study of variability of the teeth in the American Museum collection and a comparison of this known variability with the teeth of supposedly different species as figured by the earlier writers, is simple. All the

TABLE 34
MEASUREMENTS (IN MILLIMETERS) OF UNWORN CROWNS OF UPPER
PREMOLARS AND MOLARS IN *Rhinoceros*

	Greatest Width at Base	Greatest Height, Ectoloph	Ratio: Width/Height	Greatest Length, Ectoloph	Greatest Height, Ectoloph	Ratio: Length/Height
<i>R. sinensis</i>						
A.M.N.H. Nos.						
18615, P ³	55	69	0.80	47	69	0.68
18612, P ³	57	66	0.86	47	66	0.71
18626a, P ⁴	63	74	0.85	54	74	0.73
18780, P ⁴	58	64	0.91	50	64	0.78
<i>R. unicornis</i>						
Hooijer, 1946a, P ³	54-62	58-68	0.89-0.97	46-50	58-68	0.74-0.79
<i>R. sondaicus</i>						
Hooijer, 1946a, P ³	51	51	1.00	42	51	0.82
<i>R. sinensis</i>						
A.M.N.H. Nos.						
18623, M ¹	—	—	—	65	79	0.82
18612, M ²	—	—	—	63	75	0.84
18612, M ²	—	—	—	65	77	0.84
18625, M ²	—	—	—	75	84	0.89
<i>R. unicornis</i>						
A.M.N.H.(M.) No.						
54456, M ²	—	—	—	61	72	0.85
<i>R. sondaicus</i>						
A.M.N.H. (M.) No.						
146717, M ¹	—	—	—	49	53	0.93

rhinoceros material from the fissures of Szechwan belongs to a single species, *Rhinoceros sinensis* Owen. The relationships of this species are with the modern species representative of the genus *Rhinoceros*, particularly with *Rhinoceros unicornis*. With the above considerations in mind, it might be well at this place to include the remarks made by Matthew and Granger with regard to the affinities of *Rhinoceros sinensis*: "The characters of the teeth in the neotype are strongly suggestive of affinity to the Indian and Javan rhinoceroses, combining peculiarities of the two; the referred specimens bring it on the whole nearer to the Indian species . . . The neotype skull is too badly crushed to be decisive as to the characters of the occiput, and no other specimens show this region. The position of the horn, on the nasals but not quite terminal, is like *R. indicus* and unlike *Atelodus*" (Matthew and Granger, 1923, p. 572).

It is unfortunate that the skull of *Rhinoceros sinensis* is at present so imperfectly

known, with the result that most of our deductions as to the relationships of this species must of necessity be based on the structure of the dentition. It is possible, however, by combining our scanty knowledge of the skull (obtained largely from the single crushed specimen, A.M.N.H. No. 18626) with a rather abundant knowledge of the dentition (based in large part on the unusually fine series of teeth collected by Granger at Yenchingkou) to obtain a fair idea as to the zoologic position of the fossil rhinoceros from Szechwan.

So far as the skull is concerned, it would appear that *Rhinoceros sinensis* had but a slight development of the horn boss on the nasals, certainly much less than in *Rhinoceros unicornis* and very possibly less than in *Rhinoceros sondaicus*, although the crushing of the specimen makes this last point difficult to determine with certainty. However, it seems reasonably certain that the development of the nasal horn in the extinct species was no greater than in *Rhinoceros sondaicus*.

Except for this observation nothing more of importance can be said about the skull structure of the fossil.

Consequently it is necessary to turn to an examination of the dentition, and here we find the combination of the characters that Matthew mentioned but never elucidated.

There is a considerable amount of individual variation in the teeth of *Rhinoceros sinensis*, both in structural characters and in size, the latter much greater, in fact, than in either *R. sondaicus* or *R. unicornis*, both recent and fossil. Several years ago one of us (Hooijer, 1946a, 1946b) made a detailed study of the Dubois collection of prehistoric and fossil rhinoceroses from central Sumatra and Java, in which both of these species are abundantly represented by dental as well as skeletal material. *R. sondaicus* occurs in the Pleistocene fauna of Java as well as in the prehistoric fauna of Sumatra and Java; the fossil and prehistoric teeth differ from the recent mainly in their slightly superior size. *Rhinoceros unicornis* is also represented in the Pleistocene of Java. *Rhinoceros unicornis kendengindicus* Dubois, indistinguishable from the living Indian rhinoceros in cranial characters, differs from the recent form in being slightly less hypsodont, and in the fact that the posterior upper premolars have a more produced postero-internal angle, and the upper molars are comparatively narrower posteriorly. This material forms the base for the following comparison between the Yenchingkou rhinoceros and the Javan and Indian species.

The diagnostic characters of the teeth as quoted above from Matthew and Granger

are only a condensed description of A.M.N.H. No. 18628, one of the best-preserved upper dentitions of *R. sinensis* in the collection and selected as the neotype for the species. When all the rhinoceros material in the Yenchingkou collection is taken into account, this appears to be a medium-sized specimen of the dentition, with a relatively simple enamel pattern.

To begin with the upper dentition: Matthew and Granger (1923, p. 572) note that none of the specimens has the premaxilla preserved sufficiently to demonstrate the presence or absence of upper incisors. However, there is an upper incisor in the Yenchingkou collection (A.M.N.H. No. 18540). It belongs to the milk dentition, is unworn, and measures 31 mm. anteroposteriorly and 14 mm. transversely. No upper milk incisors of *R. unicornis* or of *R. sondaicus* are available for comparison; in these species the permanent upper incisor is over 50 mm. in length while the width of the crown is 15–19 mm. (Hooijer, 1946a, p. 55).

Matthew and Granger note in their diagnosis of *R. sinensis*: "p¹ small, deciduous." There is quite a variation in size in the anterior upper premolar, and some of the Yenchingkou specimens are definitely larger than their homologues in either of the recent species. Normally DM¹ has no successor in the permanent dentition of the recent species, but a skull of *Rhinoceros unicornis* [A.M.N.H. (M.) No. 54456, from Nepal, 1923] has a P¹ on the right side. The last molar in this skull has not yet erupted, but P² and P³ are already in place and worn, and DM⁴ is about to be shed. The left DM¹ is very much worn

TABLE 35
HEIGHTS (IN MILLIMETERS) OF UNWORN CROWNS OF P₃ AND M₃ IN *Rhinoceros*

	P ₃		M ₃	
	Metaconid	Entoconid	Metaconid	Entoconid
<i>R. sinensis</i>				
A.M.N.H. No. 18616	40	36	—	—
A.M.N.H. No. 18619	—	—	47	41
A.M.N.H. No. 18627	—	—	46	38
<i>R. unicornis</i>				
From Hooijer, 1946a	40–42	31–33	44–47	35–37
<i>R. sondaicus</i>				
From Hooijer, 1946a	32	25	34	25–29

TABLE 36
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH OF *Rhinoceros*
sinensis, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>											<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18783	A.M.N.H. No. 18607	A.M.N.H. No. 18780	A.M.N.H. No. 18606	A.M.N.H. No. 18612	A.M.N.H. No. 18628	A.M.N.H. No. 18622	A.M.N.H. No. 18626a	A.M.N.H. Nos. 18613, 18612, 18781	A.M.N.H. No. 18625	C.N.H.M. No. P.14160		
P ²													
L	—	26a	28a	—	—	28a	—	—	33a	—	32a	26a-32a	27a-32a
Wa	—	41	36	—	—	45	—	—	43	—	42	40-47	34-45
Wp	—	43	41	—	—	50	—	—	—	—	46	40-49	39-45
P ³													
L	38a	32a	37a ^b	35a	38a	35a	42a	—	—	—	37a	35a-43a	34a-47a
Wa	51	52	55 ^b	54	57	59	63	—	—	—	58	53-62	48-57
Wp	49	51	50 ^b	50	54	58	56	—	—	—	55	51-56	45-53
P ⁴													
L	40a	35a	38a	37a	35a	39a	38a	44a	48a	—	42a	37a-39a	35a-42a
Wa	57	57	59	59	58	65	68	67	70	—	62	62-69	51-62
Wp	52	55	55	55	53	61	58	57	64	—	58	56-60	47-59
M ¹													
L	48a	41a	42a	45a	51a	46a	55a	50a	—	50a	49a	39a-44a	35a-45a
Wa	63	64	63	68	70	70	74	—	—	81	65	58-71	51-65
Wp	59	58	61	65	65	64	67	—	—	76	59	51-62	45-56
M ²													
L	—	45a	46a	50a	57a	49a	59a	55a	60a	57a	50a	42a-50a	37a-50a
Wa	—	64	63	72	71	73	75	75	80	82	69	59-68	53-64
Wp	—	56	56	64	60	63	65	67	72	75	58	52-61	44-54
M ³													
L	—	46	—	54	56	—	53	—	—	—	49	44-49	36-51
Wa	—	57	—	62	65	—	71	—	—	—	59	53-62	43-57
Los	—	54a	—	63	67	—	68	—	—	—	56	55-64	44-62

^a See Hooijer (1946a).

^b A.M.N.H. No. 18615.

down, as usual in skulls of this age. The tooth in front of the right P², however, is only very slightly worn and is much larger than any DM¹ of *R. unicornis* or *R. sondaicus*, being 32 mm. anteroposteriorly and 30 mm. transversely. Only *R. sinensis* may have first milk molars that attain these dimensions, as shown in tables 38 and 39. Two of these are represented in figure 39 (A.M.N.H. Nos. 18782 and 18623), together with the small specimen (A.M.N.H. No. 18610).

Before entering into a discussion of the

specific characters of the premolars and molars of *R. sinensis*, we must enumerate the characters by which the dentition of *R. unicornis* differs from that of *R. sondaicus*:

1. The outer surface of the upper molars is approximately straight in *R. unicornis*, while in *R. sondaicus* there is a prominent paracone style and the outer surface is concave behind; the posterior moiety is more inclined inward and the metastyle is again raised, making the outer surface sinuate in its course.

2. In *R. unicornis* there is a vertical de-

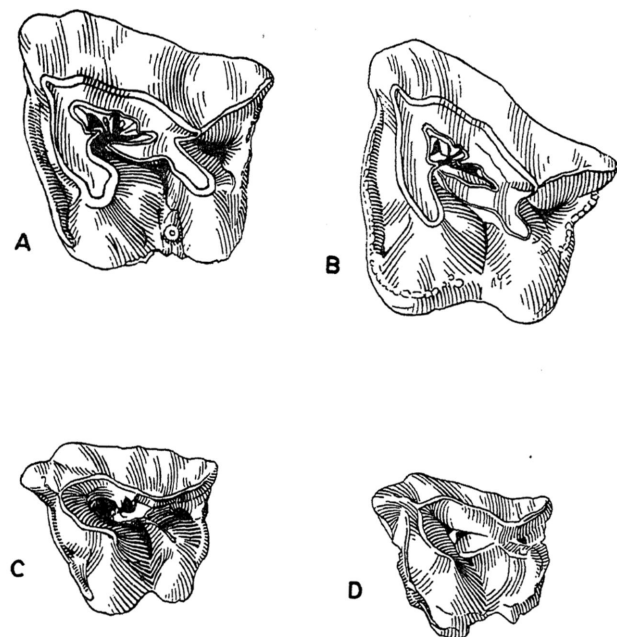


FIG. 35. A. *Rhinoceros sinensis* Owen, A.M.N.H. No. 18622, left M¹. B. *Rhinoceros plicidens* Koken (1885, pl. 6, fig. 6), M¹. C. *Rhinoceros sinensis* Owen, A.M.N.H. No. 18784, left DM⁴. D. *Rhinoceros simplicidens* Koken (1885, pl. 5, fig. 7), DM⁴. All figures three-fourths natural size.

pression in the anterior surface of the proto-loph, usually a pronounced vertical groove that is most distinct just above the anterior cingulum. This so-called protocone fold does not occur in *R. sondaicus*.

3. The inner portion of the proto-loph has a greater backward extension in *R. unicornis* than in *R. sondaicus*.

4. In *R. unicornis* there is often a crista which joins with the crochet so as to form a medifossette. This is only very exceptionally found in *R. sondaicus*.

5. The premolars and molars are more hypsodont in *R. unicornis* than in *R. sondaicus*, as shown by the comparison of the unworn crowns of P³ (Hooijer, 1946a, p. 93), M³ (pp. 97-98), P₄ (p. 102), and M₃ (p. 100).

As far as point 1 is concerned, *R. sinensis* is definitely closer to *R. sondaicus* than to *R. unicornis*. As noted by Matthew and Granger, the posterior rib (metacone style) of the outer surface is weak on M¹ and absent on M²⁻³, while all upper molars have a promi-

nent anterior rib (paracone style). Actually, the paracone style is not so prominent on the upper molars of *R. sinensis* as is typical of *R. sondaicus*, although it is definitely more pronounced than in *R. unicornis*. Also the concavity of the posterior half of the ectoloph is not quite so marked in *R. sinensis* as in *R. sondaicus*, but more so than in *R. unicornis*, with its characteristically flat ectoloph. In *R. unicornis* the posterior moiety of the ectoloph is concave only in its upper part, and near the roots the metacone style may be as marked as the paracone style, flattening towards the top of the crown. In *R. sinensis* the metacone style is weak or absent, as in *R. sondaicus*, yet the incurving of the posterior half of the ectoloph is less than in the Javan species, which seems to be a function of the lesser prominence of the paracone style in front of it. *R. sinensis* is truly intermediate between *R. sondaicus* and *R. unicornis* in the shape of the ectoloph, but closer to *R. sondaicus* than to the Indian species.

TABLE 37

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>								<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18607	A.M.N.H. No. 18623	A.M.N.H. No. 18627	A.M.N.H. No. 18628	A.M.N.H. No. 18625	A.M.N.H. No. 18626	A.M.N.H. No. 18780	A.M.N.H. No. 18787		
P ₂										
L	—	30	—	32	—	—	31	34	31-37	25-30
W	—	15	—	21	—	—	19	22	19-25	16-21
P ₃										
L	—	40	39 ^b	39	—	—	39	—	32-43	33-39
W	24	—	26 ^b	28	—	—	26	—	22-30	23-27
P ₄										
L	—	—	—	45	—	—	45	46	38	35-42
W	29	—	—	—	—	—	30	30	29-35	25-30
M ₁										
L	—	51	48	52	55	53	51	52	36-51	40-43
W	—	32	33	36	34	34	32	31	26-31	26-31
M ₂										
L	49	60	52	56	61	56	54	—	47-56	42-48
W	29	33a	33	34	37	—	32	—	27-30	26-31
M ₃										
L	51	—	56	—	—	—	—	57 ^c	49-50	39-47
W	30	—	—	—	—	—	—	34 ^c	29-33	24-28

^a See Hooijer (1946a).

^b A.M.N.H. No. 18616.

^c A.M.N.H. No. 18619.

In most of the upper molars of *R. sinensis* there is a sharply defined protocone fold, a vertical groove in the anterior surface of the protoloph that is typical for *R. unicornis* but not shown in the upper molars of *R. sondaicus*. In molars with very sharp and deep protocone folds, such as in the large dentition, A.M.N.H. No. 18625, there is also a vertical groove in the anterior surface of the metaloph, and one in the posterior surface of the protoloph. In several last upper molars of *R. sinensis* the protocone fold is so weak as to be practically absent, as, for example, the M³ in A.M.N.H. Nos. 18606 and 18607. In the upper premolars the protocone fold does not show up so well as in *R. unicornis*, but in the DM³ and DM⁴ of *R. sinensis* the protocone fold is usually well defined. Consequently, in point 2, *R. sinensis* agrees very well with *R. unicornis*.

The protoloph of the upper molars in *R.*

sinensis is more produced backward and internally than in *R. sondaicus*, agreeing very well, again, with *R. unicornis* in this respect. In a number of fossil specimens the protoloph takes up about two-thirds of the inner surface of the crown, as in *R. unicornis*, while the metaloph is relatively stronger on the inside in *R. sondaicus*. Consequently, point 3 brings *R. sinensis* again closer to *R. unicornis*.

While in many upper molars and premolars of *R. sinensis* there are several irregularly shaped, small, enamel projections from the ectoloph into the mediusinus, there is never a well-defined crista that joins the crochet so as to enclose a medifossette. The latter condition is typical for *R. unicornis*, although in this species the crista may also be rudimentary. In *R. sondaicus* the crista is normally restricted to the upper milk molars and absent in the upper molars. There is very much individual variation in the development of minor

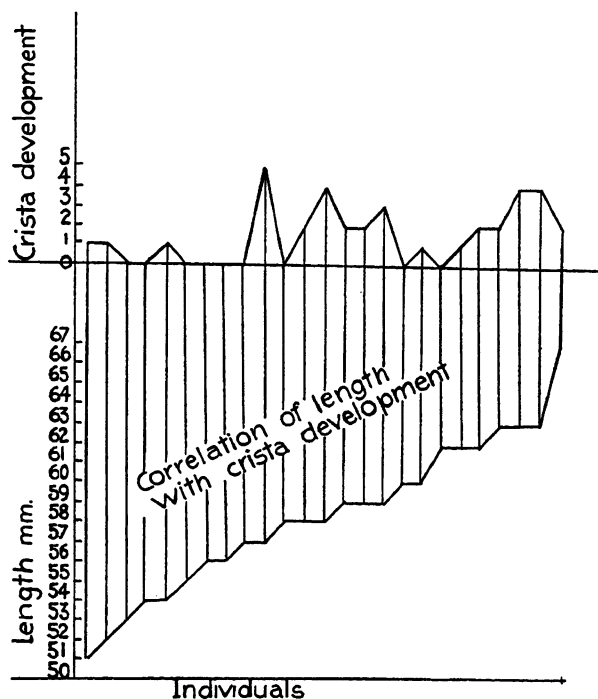


FIG. 36. Diagram illustrating correlation of length of M^1+M^2 with crista development in *Rhinoceros sinensis*.

enamel projections in the mediusinus, and the crochet may also bear several projections. In the dentition now in the Chicago Natural History Museum there is hardly any accessory enamel folding except for a duplicated crochet in the left P^4 . There is also a double crochet in both P^4 's and in the right M^1 , but not in the left M^1 , of A.M.N.H. No. 18628 (pl. 20). Cristae in the form of multiple enamel spurs are seen in the upper premolars and molars of A.M.H.N. Nos. 18606, 18622, 18626a, and 18780, and in the M^1 and M^2 of No. 18625, but in No. 18612 the two first molars show a junction of one of these small cristae with the crochet so that a medifossette will be formed upon wear. In M^3 of A.M.N.H. No. 18607 there is a distinctly developed single crista, not shown in the associated M^1 or M^2 . Some molars also have enamel projections into the post-sinus.

The cingulum is variable in development in *R. sinensis*, narrow or wide, with crenulated ledges on the anterior surface sometimes extending to the inner surface of the protoleph. There may be one to several tubercles devel-

oped in the entrance to the mediusinus, and the posterior cingulum often bears a distinct point labially to the V-shaped incision. Some upper premolars have a cingulum all along the inner surface, while others completely lack the cingulum on the inside.

All these variations are found in *R. unicornis* and *R. sondaicus*. In the rudimentary development of the crista and its general lack of juncture with the crochet, *R. sinensis* is somewhat closer to *R. sondaicus* than to the Indian rhinoceros. The heavier development of the crochet, however, brings *R. sinensis* again nearer to the Indian rhinoceros, in which the crochet is stronger than in *R. sondaicus*. In point 4, consequently, we see a condition in the fossil Chinese species that is intermediate between that in the two living species of *Rhinoceros*.

Matthew and Granger (1923, p. 572) remark that the teeth of *R. sinensis* are moderately hypsodont, slightly less so than in *R. unicornis*. The comparison between unworn crowns of homologous teeth in *R. sinensis*, *R. unicornis*, and *R. sondaicus* shows that the

TABLE 38

MEASUREMENTS (IN MILLIMETERS) OF THE UPPER MILK TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>											<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18610	A.M.N.H. No. 18758	A.M.N.H. Nos. 18581, 18623, 18613, 18612	A.M.N.H. Nos. 18623, 18628	A.M.N.H. Nos. 18547, 18623, 18780	A.M.N.H. Nos. 18613, 18617	A.M.N.H. Nos. 18782, 18623, 18470, 18626	A.M.N.H. Nos. 18782, 18628, 18626, 18613	A.M.N.H. No. 18782	A.M.N.H. No. 18623	A.M.N.H. No. 18625		
DM ¹													
L	25	26	30	—	—	—	32	34	32	33	—	22a-28a	20a-25
W	20	21	23	—	—	—	27	28	28	27	28	23-25	18a-24
DM ²													
L	28a	30a	29a	—	30a	33a	34a	34a	37a	36a	—	31a	26a-30a
Wa	32	34	36	38	39	39	41	43	43	40a	—	38a	33-36
Wp	36	37	37	37	39	40	43	45	45	46	47	38-39	32-37
DM ³													
L	35a	37a	37a	38a	40a	—	39a	37a	44a	45a	43a	36a-39a	33a-41a
Wa	45	46	49	50	51	—	52	55	54	57	—	46	40-46
Wp	44	43	46	46	47	—	47	50	53	51	54a	41-42	35-43
DM ⁴													
L	39a	—	40a	38a	41a	40a	44a	—	—	—	44a	38a-45a	34a-44a
Wa	49	—	50	51	52	52	59	—	—	—	61	49-56	41-51
Wp	46	—	47	49	49	50	54	57	—	—	58	48-50	38-50a

^a See Hooijer (1946a).

TABLE 39

MEASUREMENTS (IN MILLIMETERS) OF THE LOWER MILK TEETH OF *Rhinoceros sinensis*, *unicornis*, AND *sondaicus*

	<i>R. sinensis</i>					<i>R. unicornis</i> ^a	<i>R. sondaicus</i> ^a
	A.M.N.H. No. 18623	A.M.N.H. No. 18623	A.M.N.H. No. 18758	A.M.N.H. No. 18782	A.M.N.H. No. 18626		
DM ₁							
L	—	—	20	—	—	19-21	14-18
W	—	—	10	—	—	11	10-11
DM ₂							
L	30	31	30	31	—	31-33	25-29
W	15	17	17	16	18	18-19	14-16
DM ₃							
L	45	44	42	43	—	42-46	37-43
W	22	24	22	22	26	23-24	20-23
DM ₄							
L	—	—	43	43	—	43-45	38-42
W	26	—	23	23	29	23-25	22-24

^a See Hooijer (1946a).

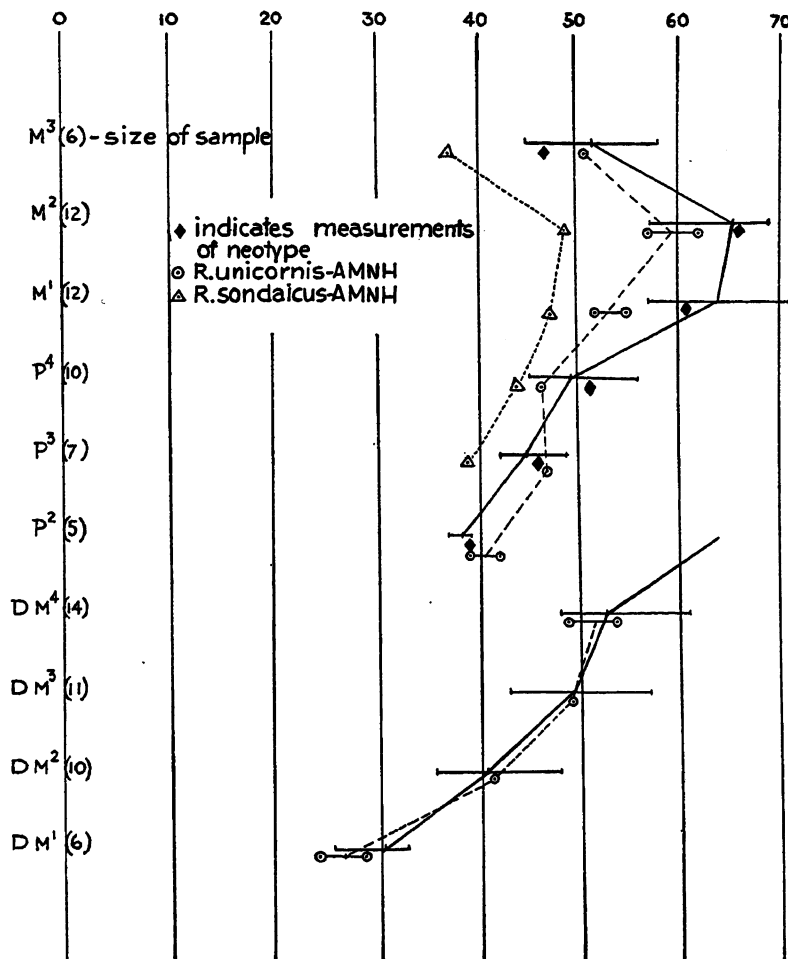


FIG. 37. Diagram comparing length of upper dentition in *Rhinoceros sinensis*, *R. unicornis*, and *R. sondaicus*. Horizontal lines represent observed ranges.

fossil Chinese species is more hypsodont than *R. sondaicus* but compares closely with *R. unicornis* in crown height, although some of the fossil teeth are even more hypsodont than their homologues in the Indian species, as far as the comparative material goes.

In three unworn M³'s of *R. sinensis* the ectoloph is either slightly shorter or slightly longer than high:

	LENGTH	HEIGHT
A.M.N.H. No. 18606	63 mm.	68 mm.
A.M.N.H. No. 18785	66	70
A.M.N.H. No. 18612	67	64

In summary, *Rhinoceros sinensis* agrees with *R. unicornis* in having a protocone fold

in the upper molars; in the fact that the inner portion of the protoloph is much expanded posteriorly, and in the degree of hypsodonty of the upper and lower premolars and molars. On the other hand, *R. sinensis* is closer to *R. sondaicus* in the shape of the ectoloph, although this is not quite so sinuate as it is in the Javan species, and in the rudimentary development of the crista, although the crochet is stronger than it is in *R. sondaicus* and more like that in *R. unicornis*.

The measurements of the upper and lower permanent and milk teeth of *R. sinensis* are presented in tables 34 to 39. The ranges of variation of the measurements in the two

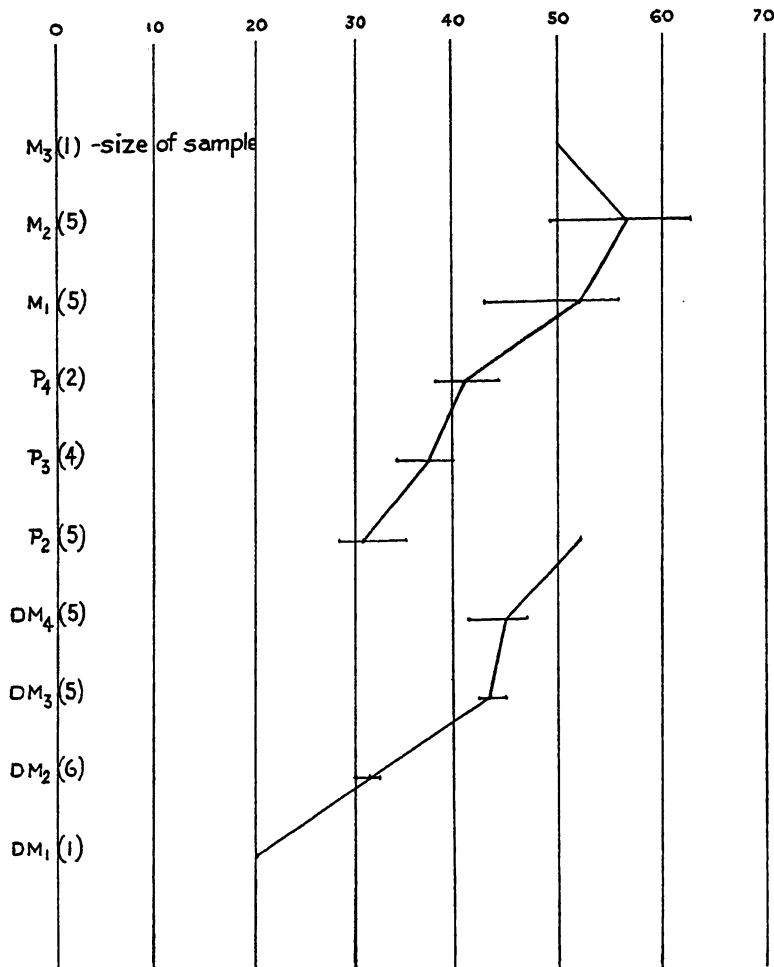


FIG. 38. Diagram of length of lower dentition in *Rhinoceros sinensis*. Horizontal lines represent observed ranges.

recent species, *R. unicornis* and *R. sondaicus*, are taken from Hooijer (1946a) and include both the recent and the fossil teeth, while some measurements were added from the recent *R. unicornis* skulls [A.M.N.H. (M.) Nos. 54454, 54456, and 70445]. The anteroposterior diameters of the teeth are taken at the base of the crown; in the upper teeth, at the base of the ectoloph except for M⁸ where this measurement was taken on the inner surface. The transverse diameters are also taken at the base of the crown, and the ratio given for the upper molars is that between the posterior width and the anterior width. It will be seen that the range of variation in *R. sinensis* often is greater than in the recent teeth, and that many Chinese teeth exceed

those of the two recent species in size. There is, however, a gradation in size from the smallest to the largest teeth in the Yenching-kou series, and it seems unnecessary to accept the presence of more than one species of *Rhinoceros* at this site. The text figures (figs. 35, 39, 40) and the various photographs (pls. 20-22) of more or less complete dentitions show the variability in these teeth from relatively simple to relatively complex enamel patterns.

The lower dentition of *R. sinensis* needs little comment. There is a lower incisor in this species, as shown by milk teeth *in situ* in the mandible of A.M.N.H. No. 18626 and several isolated milk incisors in Nos. 18540 and 18780. They measure about 20 mm. by

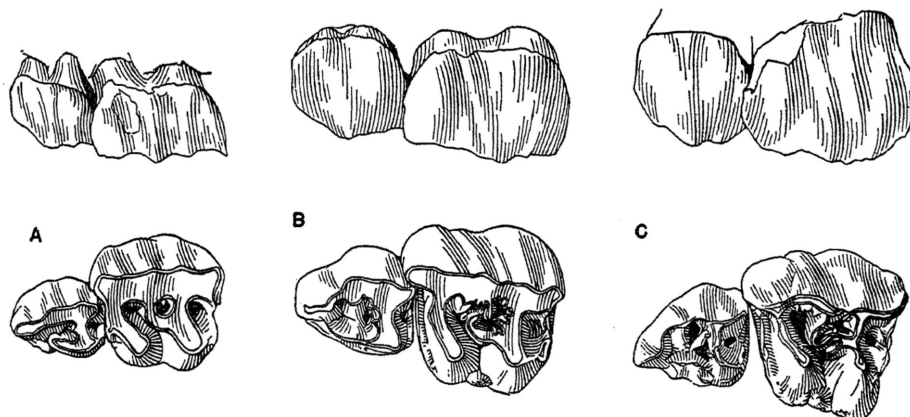


FIG. 39. *Rhinoceros sinensis* Owen. Three left DM^{1-2} , to show variability. Lateral and crown views. A. A.M.N.H. No. 18610. B. A.M.N.H. No. 18782. C. A.M.N.H. No. 18623. One-half natural size.

15 mm. in cross section; the alveoli of the deciduous lower incisors in a specimen of *R. sondaicus* measure 17 mm. by 13 mm. (Hooijer, 1946a, p. 62). One permanent lower incisor in the Yenchingkou collection (A.M.N.H. No. 18780, of the left side) measures 29 mm. by 21 mm. in cross section.

Some of the teeth show interesting variations. The posterior valley of DM^2 is either open or closed on the inside (A.M.N.H. Nos. 18781 and 18623, respectively), while intermediate conditions also occur (A.M.N.H. No. 18539, where the lingual wall to the posterior valley is only partially formed). This type of variation is known from the recent species as well (Hooijer, 1946a, p. 32). DM_4 in a left mandibular ramus (A.M.N.H. No. 18757) has the anterior valley closed on

the inside by an enamel wall that swings inward and backward from the protoconid, thus forming an isolated pit. Similar extra formations are seen both in the right and in the left P_2 of the mandible A.M.N.H. No. 18623 (fig. 40). In this case the posterior valley is closed on the inside by an enamel wall, which is more complete in the left than in the right specimen. The right and left P_3 of A.M.N.H. No. 18780 are peculiar in having the metaconid constricted so as to form an isolated cusp. A normal P_3 (A.M.N.H. No. 18616) is figured beside the anomalous specimen for comparison. The crowns of the lower premolars and molars, as already stated above, are as high as, if not even higher than, those of *R. unicornis* when unworn.

It seems evident from the above discussion

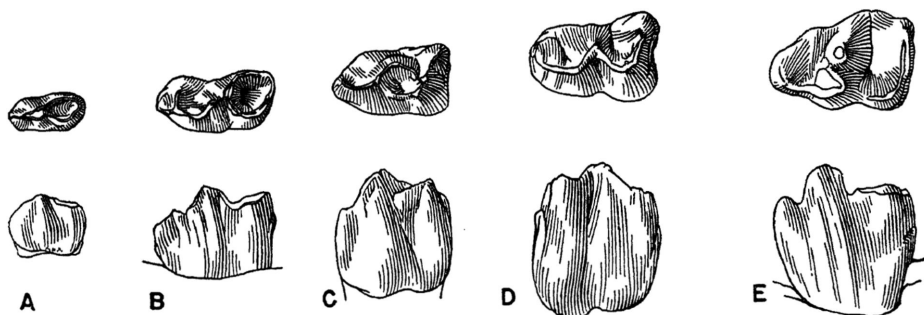


FIG. 40. *Rhinoceros sinensis* Owen. A. A.M.N.H. No. 18758, left DM_1 . B. A.M.N.H. No. 18623, left DM_2 . C-E. A.M.N.H. Nos. 18623, 18787, and 18780, respectively, left P_2 , to show variability. Crown and lateral views. One-half natural size.

of its characters that *R. sinensis* occupies a more or less intermediate position between the Javan and the Indian species. One of us (Colbert, 1942b) has expressed the view that *R. sondaicus* may be considered a persistent primitive species from which, as a structural ancestor, *R. sinensis* arose. Further evolutionary development, from either *R. sinensis* or a closely related form descendent from the *R. sondaicus* type, led to the separation probably through *R. sivalensis* or *R. unicornis*.

In the skeleton of *R. sondaicus* there is seen a progression into the present graviportal type. In the Pleistocene of Java the humerus and femur were shorter, but the radius, tibia, and metapodials were longer, than in the recent animals. The Pleistocene type is mediportal as is the recent Sumatran rhinoceros (Hooijer, 1946b). The single preserved femur in the Yenchingkou collection (A.M.N.H. No. 18609) is strikingly small, being 397 mm. long from caput to medial condyle against 438–495 mm. in eight specimens of *R. sondaicus*, and with a proximal width of 142 mm. against 171–219 mm. in 10 specimens of *R. sondaicus* (Hooijer, *ibid.*, p. 72), and two third metatarsals (A.M.N.H. No. 18623) measure 175 and 176 mm. in median length against 150–155 mm. in four recent, and 165 mm. in a fossil third metatarsal of *R. sondaicus* (Hooijer, *ibid.*, p. 81).

ARTIODACTYLA

SUIDAE

SUS LINNAEUS

Sus LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 49.

GENERIC TYPE: *Sus scrofa* Linnaeus.

DIAGNOSIS: Skull long, high, and narrow, without osseous tuberosities above or on sheaths of upper canines; full dentition may be present, or there may be a reduction by suppression of I3 and P1; canines directed outward, cheek teeth brachyodont. Four complete toes in both fore and hind feet, glenoids raised and paroccipital processes very long.

Sus scrofa Linnaeus

Sus scrofa LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 49.

Sus scrofa, LYDEKKER, 1915, *Catalogue of the ungulate mammals in the British Museum*, vol. 4,

p. 308. (This source gives the full history of the synonymy of the species, which is long and involved and need not be repeated here.)

REFERRED SPECIMENS: A.M.N.H. Nos. 18437, a left fourth metacarpal; 18438, skull and jaw, lacking the zygomatic arches and the tip of the snout, but with deciduous molars and first permanent molars, above and below, erupting; 18441, lower canine; 18442, right and left radius, right third metacarpal, left third metatarsal, M₁; 18443, left maxilla with DM²⁻⁴, M¹, right mandibular ramus with DM₄, M₁; 18444, skull, lacking the arches, bullae, and paroccipital processes but possessing the right P²-M¹, and the left P⁴-M², and the broken bases of other teeth; 18445, skull and jaw, lacking portions of the snout, the bullae, the paroccipital processes, and the lower borders and angles of the jaws; the teeth present are the left canine, P¹-M², right P²-M², broken incisors and canines in the lower jaw, and P₂-M₃ on both sides; 18447, fragments of right maxilla with P⁴-M², left maxilla with P⁴-M² and M² loose, right mandibular ramus with P₂₋₃ erupting and M₁₋₂; 18463, back of right mandibular ramus with M₂₋₃; 18555d, symphysis with deciduous and permanent incisors; 18581, lower incisors, upper canine; 18582, left half of symphysis with I₂ and canine; 18759, skull and jaw, the skull lacking the tips of the nasals, the left zygomatic arch and the left paroccipital process, and the jaw the right ascending ramus; teeth present are the first upper incisors, right canine, right and left P¹-M², all lower teeth except right P₁; 18760, skull and jaw of a juvenile, the skull lacking the right zygomatic arch, the basicranium, and the front of the snout, the jaw lacking the ascending rami; the following teeth are present on both sides, DM²⁻⁴, M¹ in alveolus, DM₃₋₄, M₁ in alveolus; 18761, front of skull with right canine in alveolus, DM¹⁻³, and left DM¹⁻⁴, M¹; 18762, left premaxilla with I²⁻³, left maxilla with P¹⁻³; mandible lacking the ascending rami, but with canines, right P¹-M² and left P²-M²; 18788, left ramus fragment with canine, P₂-M₂; 18789, right and left rami with DM₂₋₄, M₁; 18790, palate and mandible of juvenile with right DM³⁻⁴, left DM²⁻⁴, right and left DM₃₋₄; 18791, right ramus with P₄-M₃; 18792, right ramus fragment with

TABLE 40
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF *Sus scrofa*

	Condylobasal Length	Palatal Length	Zygomatic Width	Occipital Width	Width Outside Last Upper Molars	Upper Cheek Teeth	Lower Cheek Teeth
<i>S. scrofa</i>							
Yenchingkou							
A.M.N.H. Nos.							
18444	—	—	—	72e	77	121	—
18445	330e	—	130	60	76	123	130
18759	316	218	143	64	70	129	148
18762	—	—	—	—	—	—	149
<i>S. s. chirodonta</i>							
9 specimens							
Max.	354	248	164	83	78	128	139
Min.	295	199	132	65	66	113	123
Mean	322	221	147	73	72.8	121	132
<i>S. s. moupinensis</i>							
2 specimens							
Max.	331	230	156	64	78	122*	140
Min.	—	220	143	64	72	115	140
Mean	—	225	149.5	64	75	118.5	140

* Three specimens.

M₁₋₃; 18793, right maxilla with P³-M², M³ in alveolus; right ramus with broken canine, P₄-M₂, M₃ in alveolus; left ramus with P₄-M₂, M₃ in alveolus; 18794, right DM⁴, M¹; 18795, right DM³⁻⁴, M¹; 18796, symphysis with incisors and right canine, P₁, portion of right ramus with P₄-M₃; 18797, left maxilla with P²-M²; 18798, right maxilla with P³-M², M³ in alveolus. C.N.H.M. Nos. P.14149, mandible and palate, associated, with right P²-M³, left P²-M², and right P₃-M₂, left P₂-M₃; P.14150, right maxilla with P³-M³; P.14151, left mandibular ramus with P₂-M₃.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Of medium to large size; lower canine with outer surface markedly less in width than posterior surface, which is oblique, and next in width to inner surface; last molar large, with third ridge.

DISCUSSION

In 1923 Matthew and Granger figured the skull and jaws of a pig from Yenchingkou (A.M.N.H. No. 18445, listed above). In the legend to their figure this specimen was identified as "*Sus* sp. cf. *hyotheroides* Schl."

No discussion of suid remains from Szechwan was attempted by these authors, who confined themselves to the following remarks: "This is a species about the size of the modern *Potamochoerus* but p⁴ is larger and more complex" (Matthew and Granger, 1923, p. 594).

Therefore it is quite evident that Matthew and Granger had devoted only the most superficial kind of examination to the suid remains from Szechwan when their preliminary contribution was written.

Sus hyotherioides is definitely a Pliocene form from China and as such is characterized by its less advanced anatomical features as compared with Pleistocene and recent species. This is particularly apparent in the dentition, where in *Sus hyotherioides* the last lower premolars lack the elevation of the anterior cusps and the third molars lack the elongation of the tooth and the complexity of the heel that are so characteristic of the recent *Sus scrofa* and, incidentally, of the pig from the Yenchingkou fissures.

Thus in a detailed comparison of the fossil remains from Szechwan with other fossils and with recent pigs of Asia it soon became ap-

TABLE 41
LENGTH (IN MILLIMETERS) OF CERTAIN TEETH IN *Sus scrofa*

	Upper C	Lower C	DM ⁴	DM ₄	M ¹	M ₁	M ²	M ₂	M ³	M ₃
A.M.N.H. Nos.										
18438	—	—	13.5	18.5	18.6	18.2	—	—	—	—
18441-3	—	21.5	18.0	22.7	20.8	20.7	—	—	—	—
18444	22e	—	—	—	15.6	—	20.7	—	35.6	—
18445	18.6	18.0	—	—	17.0	16.2	23.5	21.7	34.4	35a
18447	—	—	—	—	20.5	19.0	24.7	25.5	41.5	—
18463	—	—	—	—	—	—	—	20.3	—	31.0
18759	14+	14.0	—	—	19.3	18.6	26.3	25.6	38e	40e
18760	—	—	17.8	25.0	21a	21.0	—	—	—	—
18761	—	—	16.0	—	20.0	—	—	—	—	—
18762	—	14.2	—	—	—	17.5	—	22.3	—	41.0
18788	—	13.3	—	—	—	17.0	—	22.5	—	—
18789	—	—	—	20.0	—	17.4	—	—	—	—
18790	—	—	15.3	22.4	—	—	—	—	—	—
18791	—	—	—	—	—	16.0	—	20.5	—	37.0
18792	—	—	—	—	—	14.5	—	20.5	—	35.6
18793	—	12.0	—	—	17.2	16.4	22.5	22.5	—	—
18794	—	—	14.4	—	17.3	—	—	—	—	—
18795	—	—	13.8	—	16.9	—	—	—	—	—
18796	—	10.5	—	—	—	15.3	—	20.8	—	39.0
18797	—	—	—	—	16.7	—	23.2	—	—	—
18798	—	—	—	—	18.0	—	23.3	—	—	—
C.N.H.M. Nos.										
P.14149	—	—	—	—	19.5	—	26.5	—	44.5	—
P.14150	—	—	—	—	17.0	—	22.5	—	33.5	—

parent that the Yenchingkou form was close to *Sus scrofa*. Indeed a careful comparison of the fossil material with some of the recent suids of this species from southern China, such as *Sus scrofa moupinensis* and *Sus scrofa chirodonta*, fails to reveal any significant characters that would serve for separating the fossil from the recent forms, a fact the quantitative aspects of which are shown graphically in tables 40 and 41 and figure 41.

For instance, the fossil pig from Yenchingkou has the facial elongation so characteristic of *Sus scrofa*. The orbit is far back, its posterior portion being over the hinder portion of the last molar. The occiput is high, with the basicranial region raised accordingly. The auditory bullae are very deep, and the paroccipital processes are long. The mandible is long, with a high ascending ramus. The first two upper incisors are enlarged, as is typical of *Sus scrofa*. The cheek teeth also are characteristic of this species,

showing in the molars a great complexity of the enamel folding of the cusps. In the fourth lower premolars, as is characteristic of *Sus scrofa*, the central cusp is bifid, the two portions being arranged longitudinally, with the posterior portion somewhat internal to the anterior one, while the back of the tooth is very high. The canines are of the usual *Sus scrofa* form—moderately large in certain individuals which supposedly were males, rather small in others, presumably females. The lower canine of the male, as exemplified in A.M.N.H. Nos. 18759 and 18441, is of "scrofic" form in cross section, with the posterior face of the tooth next in length to the internal face. It might be said that this tooth in the fossil shows a rather compressed scrofic cross section.

One comparison remains to be made, namely, with *Sus lydekkeri* Zdansky, from the Pleistocene of northern China. However, the differences between the Yenchingkou fossil and this last-named species are suffi-

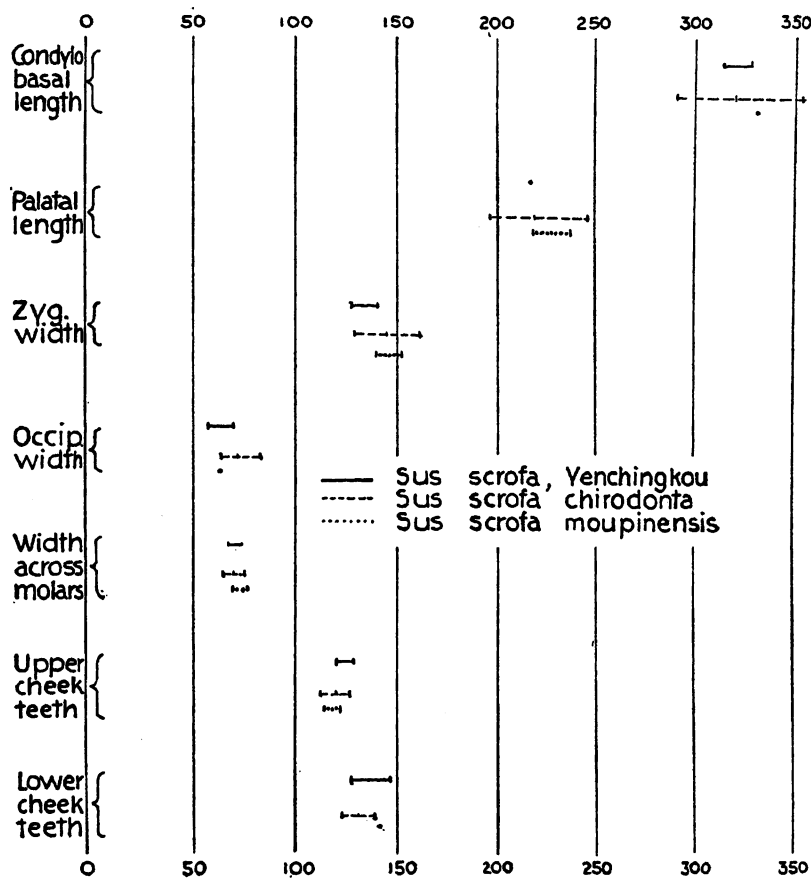


FIG. 41. Diagram of comparative measurements of specimens of *Sus scrofa* from Yenchingkou, with two Recent subspecies.

ciently great that the two forms may be considered as validly separable. *Sus lydekkeri* is a robust type, seemingly larger than the Yenchingkou fossil, and is characterized especially by its very large, heavy canines.

Because of the extraordinarily close resemblances in all respects between the fossil pig from Yenchingkou and the modern Asiatic representatives of *Sus scrofa*, the fossil is unhesitatingly identified as belonging to this species, without an attempt at a subspecific designation.

CERVIDAE

RUSA SMITH

Rusa C. H. SMITH, 1827, in Griffith, The animal kingdom . . . by . . . Cuvier, vol. 4, p. 105.

GENERIC TYPE: *Cervus unicolor* Kerr.

DIAGNOSIS: Antlers stout and rugose,

rounded in cross section, three-tined, with the brow tine forming an acute angle with the beam. Molars hypsodont, with small accessory inner columns in the upper, and outer columns in the lower, molars. Enamel faintly sculptured.

Rusa unicolor (Kerr)

Cervus (Rusa) unicolor, Lydekker, 1915, Catalogue of the ungulate mammals in the British Museum, vol. 4, p. 70. (This source gives the full history of the synonymy of the species, which is long and involved and need not be repeated here.)

REFERRED SPECIMENS: A.M.N.H. Nos. 18499a, proximal portion of antler; 18537a, left mandibular ramus, with DM₃₋₄, M₁₋₂; 18538a, tine of antler; 18549, cranium with pedicles, but lacking the muzzle, zygomatic arches, and antlers; 18551, crushed palate with left P⁴-M³ and left mandibular ramus

with M_{1-3} , also isolated teeth and several phalanges; 18552, crushed portion of a skull with a left molar, also two right mandibular rami, one with P_2-M_3 , the other with M_{2-3} , various antler fragments and a right metacarpal III-IV, a right mandibular ramus with P_4-M_3 ; 18553c, right mandibular ramus with M_{2-3} ; 18554, mandibular rami, associated, with right P_2-M_3 and left P_3-M_2 , and a left mandibular ramus with P_3-M_3 ; 18555, three mandibular rami, (a) right DM_{2-4} , (b) right DM_{2-4} , (c) left P_3-M_2 ; 18561, palate and jaws, associated, with right P^{2-4} , left P^2-M^2 , right P_2-M_1 , left P_2-M_2 , also a left maxillary with M^{1-3} , four mandibular rami, (a) left M_{1-3} and right M_{2-3} , probably associated, (b) right M_{1-3} , (c) left M_{2-3} and a left metatarsal III-IV; 18563, three mandibular rami, (a) right DM_{2-4} , (b) right DM_{3-4} , (c) left DM_{3-4} ; 18565, four maxillae, (a) left M^{2-3} , (b) left P^4-M^3 , (c) left P^{2-4} , (d) right P^{2-4} ; 18571, proximal portion of left antler; 18573, right maxillary with P^4-M^3 ; 18649, tine of antler; 18799, right maxilla with P^{2-4} erupting, DM^4 , M^{1-3} , mandibular rami with right M_{1-3} , left DM_{3-4} , M_{1-3} , associated; 18800, left mandibular ramus with M_{1-3} ; 18801, broken right maxilla with M^{2-3} and mandibular ramus with M_2 and roots of other lower teeth; 18802, right mandibular ramus with DM_{3-4} , M_{1-3} ; 18803, cranium of female, lacking muzzle, teeth, and zygomatic arches; 18804, palate with right and left DM^{2-4} , M^{1-3} ; 18805, left maxilla with DM^{3-4} and left mandibular ramus with DM_{3-4} ; 18806, base of antler; 18807, right mandibular ramus with DM_{3-4} , M_{1-3} ; 18808, left mandibular ramus with P_4-M_3 ; 18809, left mandibular ramus with DM_{2-4} , M_{1-3} ; 18810, left maxilla with DM^{2-4} , M^{1-2} ; 18811, base of antler; 18812, base of antler; 18813, frontals with right antler and base of left antler; 18814, skull, lacking muzzle, teeth, and zygomatic arches, but with the proximal portions of the antlers; 18815, right antler; 18816, skull, lacking muzzle, teeth, and antlers, but with antler pedicles; 18817, right mandibular ramus with DM_{3-4} , M_1 erupting; 21785, right portion of skull with P^2-M^3 and right mandibular ramus with P_4-M_2 ; 21789, right and left mandibular rami with M_{2-3} ; 21791, left pedicle and base of antler.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Large deer with stout, rugose antlers; brow tine long, making an acute angle with beam; outer tine of terminal fork forming continuation with beam.

DISCUSSION

The sambar is widely distributed in the Oriental region, and its range extends northward into Szechwan. In Pocock's revision of the genus *Rusa* the subspecies from Szechwan, *Rusa unicolor dejeani* (Pousargues), is held identical with *Rusa unicolor equina* (Cuvier) from Sumatra, and this form differs from the Indian race, *Rusa unicolor nigra* (Blainville), in that the antlers are much shorter, with the front-outer tine of the terminal fork generally a suberect continuation of the beam, and larger than the hind-inner tine which is inclined backward and inward (Pocock, 1942, p. 517). In the Indian subspecies the large antlers have the two terminal tines very commonly subequal in length, or the hind-inner tine may exceed the front-outer in length and have an equal claim to be a continuation of the beam. Six variations are figured by Pocock (1943, p. 31).

The most complete (right) antler in the Yenchingkou collection (A.M.N.H. No. 18815) has the front-outer of the terminal tines clearly continuous with the beam, and the hind-inner tine, broken off to a great extent, is directed backward and inward, so that it resembles antlers in the recent skulls of *Rusa unicolor equina* and *Rusa unicolor dejeani*. As far as our material goes there is a size difference between the recent and the fossil antlers; the greatest diameter of the beam above the brow tine in one of the fossil antlers (A.M.N.H. No. 18571) is greater than in the recent (53 mm. against 43-47 mm.), and the length from burr to second fork in another fossil antler (A.M.N.H. No. 18815; 435 mm.) exceeds that in the recent (315-405 mm.). However, with more recent material for comparison it might very well turn out that the dimensions of the fossil antlers are within the variation limits of the recent form from the same area. The skull measurements provide no differences, and the teeth, of which much more material is available, are almost in-

TABLE 42
MEASUREMENTS (IN MILLIMETERS) OF THE SKULL OF RECENT AND
FOSSIL *Rusa unicolor*

	A.M.N.H. Nos. 18814, 18571 Yenchingkou, ♂	A.M.N.H. Nos. 18549, 18815 Yenchingkou, ♂	A.M.N.H.(M.) No. 87615 Indo-China, ♀	A.M.N.H.(M.) No. 16586	A.M.N.H.(M.) No. 43062 Yunnan, ♂	A.M.N.H.(M.) No. 43061 Yunnan, ♀
Length from posterior end of nasals to summit of occiput	187	—	182	179	211	181
Postorbital width (at base of pedicles in male)	127	116	77	113	132	78
Width of occiput	112	105	95	106	131	95
Height of occiput, from basion	83	80	80	79	85	78
Anterior-posterior diameter of beam above burr	59	59	—	56	64	—
Greatest diameter of beam above brow tine	43	44	—	47	43	—
Length from burr to second fork	—	435	—	315	405	—

TABLE 43
MEASUREMENTS (IN MILLIMETERS) OF THE TEETH OF RECENT AND FOSSIL *Rusa unicolor*

	P ² -M ³ L	M ¹ - ³ L	P ₂ -M ₃ L	M ₁ - ₃ L
A.M.N.H. Nos.				
18551	—	65	—	—
18552	—	—	118	72
18552	—	—	—	65
18554	—	—	128	78
18554	—	—	—	73
18561	—	76	—	81
18561	—	—	—	76
18565	—	65	—	—
18573	—	69	—	—
18799	—	—	—	76
18800	—	—	—	70
18807	—	—	—	72
18808	—	—	—	71
21785	—	65	—	—
A.M.N.H.(M.) Nos.				
16586	102	58	111	67
87615	111	67	122	78
43062	114	69	125	78
43061	112	68	120	74

variably within the recent range. Consequently the sambar does not seem to have undergone a diminution in size since the time of the deposition of the remains in the Yen-chingkou pits, in contradistinction to the smaller deer species. Measurements are given in tables 42 and 43.

There is one antler pair on a piece of the frontal in the Yen-chingkou collection (A.M.N.H. No. 18813) on which a great many scratches and cuts are seen, especially on the right brow tine, on the beam of the right antler, and near the base of the beam of the left antler, which is broken off a few centimeters above the brow tine. The specimen is figured in this paper (pl. 27) and has already been discussed in great detail by one of us (Hooijer, 1951b). It is of interest that Granger (1932, pp. 517-518) discussed a similar antler specimen under the head "Evidence of contemporary human occupation." It seems safer, however, to regard the working on our antler specimen, which almost certainly dates from the time when fossilization had not yet set in, as gnawings by rodents, although it is strange that no other specimen in the Yen-chingkou collection shows these marks.

MOSCHUS LINNAEUS

Moschus LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 66.

GENERIC TYPE: *Moschus moschiferus* Linnaeus.

DIAGNOSIS: Small cervids without antlers, upper canines long in males, no depression of the lacrimal bone, molars hypsodont, the lower molars with a double fold in metaconid.

Moschus moschiferus plicodon, new subspecies

TYPE: A.M.N.H. No. 18564, a skull, lacking the top of cranium, the muzzle, and the left zygomatic arch, but with right P^3-M^3 and left P^2-M^3 ; also a right mandibular ramus, probably not associated with the skull, containing P_4-M_3 .

PARATYPES: A.M.N.H. Nos. 18763, mandibular rami with right P_3-M_3 and left M_{1-3} ; 18553b, left mandibular ramus with P_2-M_3 ; 18556a, right mandibular ramus with M_{1-3} ; 18566, four left mandibular rami, (a) M_{1-3} , (b) M_{1-2} , (c) P_4-M_3 , (d) DM_4 ,

M_{1-2} ; 18577a, left mandibular ramus with DM_4 , M_{1-3} ; 18580, right maxilla with P^4-M^3 , also two mandibular rami; (a) right P_{3-4} , (b) left P_4-M_2 ; 39167, right mandibular ramus with DM_{3-4} , M_{1-2} ; 39168, right mandibular ramus with M_2 ; 39169, left mandibular ramus with DM_{3-4} , M_{1-2} ; 39170, three mandibular rami, (a) left M_{1-2} , (b) left M_3 , (c) left M_{1-2} . Certain limb bones may be referable to this species.

DIAGNOSIS: Similar to other subspecies of *Moschus moschiferus*, but with cingular folds of lower molars more strongly developed than in other forms.

DISCUSSION

The skull (A.M.N.H. No. 18564) is so similar in all its parts to recent skulls of *Moschus moschiferus* that there can be no doubt that it is conspecific with the recent musk deer. The fossil skull is no larger than skulls of recent musk deer. Two subspecies of *Moschus moschiferus* are living in China today (Allen, 1940, pp. 1129-1137), and Yen-chingkou is well within the range of one of them, viz., *Moschus moschiferus sifanicus*, while *M. m. moschiferus* inhabits northeastern China and Mongolia. In the skull the two forms can be distinguished by the shape of the lacrimal bone, which is longer anteroposteriorly than high in *M. m. sifanicus*, while the opposite is true in the typical subspecies. In the Yen-chingkou skull the lacrimal sutures fortunately are well shown, and the lacrimal is decidedly higher than long, thereby agreeing with *M. m. moschiferus* rather than with the subspecies today living in the same area. The lacrimal in the fossil skull is even higher than the maximum found in the recent form, as shown in these dimensions (ranges after Flerov, 1930):

	ANTERO- POSTERIOR	VERTICAL
Yen-chingkou	19 mm.	26 mm.
<i>M. m. moschiferus</i>	12.7-19.9	17.5-23.6
<i>M. m. sifanicus</i>	19.0-23.5	17.6-20.7

While the fossil skull does not differ in general from the recent skulls, the teeth and some of the lower jaws tend to be slightly larger.

The premolars in A.M.N.H. No. 18580 (two lower jaw fragments) are small when

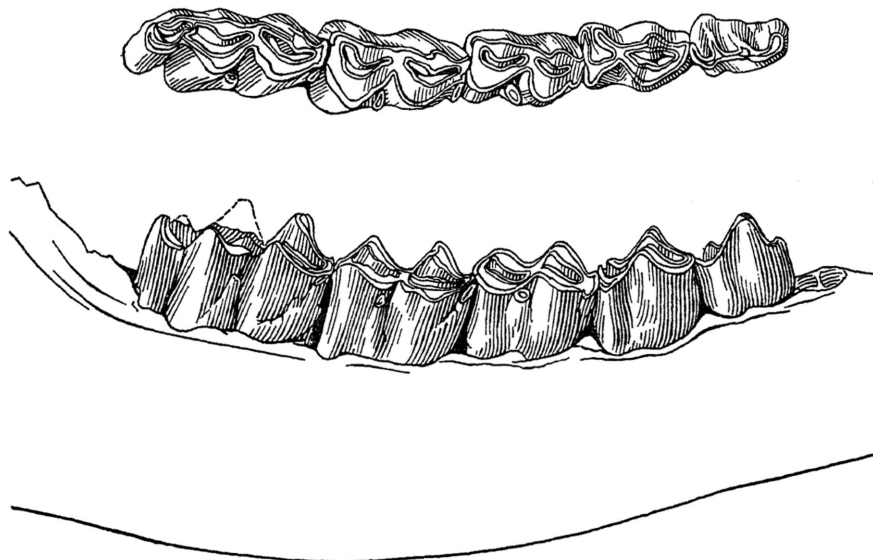


FIG. 42. *Moschus moschiferus plicodon*, new subspecies. A.M.N.H. No. 18763, right mandibular ramus with P_3 - M_3 . Crown and lateral views. Twice natural size.

compared with the other specimens, but the difference is not great.

In the manuscript left by Matthew and Granger, it is stated that the premolars of one pair of lower jaws (A.M.N.H. No. 18763) differ from recent premolars in that the pattern is simpler and more generalized, P_3 having the transverse crests less developed, while P_4 lacks all the extra crests seen in recent fourth lower premolars of *Moschus moschiferus*. The study of the other specimens in the collection shows that this difference is not constant; in A.M.N.H. Nos. 18553 and 18564 the premolars are as complex as in recent animals. The premolars and molars of A.M.N.H. No. 18763 show a very weak development of the double fold of the metaconid, the "tragulid" fold so characteristic of the lower molars in *Moschus* (Rütimeyer, 1883, p. 29, pl. 6, figs. 40, 41). However, in other specimens the double fold of the metaconid is distinctly developed, and there is variation in this respect in the recent lower molars.

The external pillars and anterior cingular folds vary greatly in development in the fossil lower molars, and in some they are stronger than in recent material at hand.

The *Moschus* sp. from locality 18 near

Peiping described by Teilhard de Chardin (1940, p. 78) is stated to differ from the recent form only in its somewhat larger size. The length of the molars is given as 28 mm., which is greater than in any recent or fossil specimens that we have studied.

Young (1932a, p. 19) has described the Choukoutien *Moschus* as *M. moschiferus* var. *pekinensis* because it has the upper premolars and molars provided with an accessory spur on the internal side of the inner crescent (of the posterior lobe in the molars) and also on the basis of the more developed cingular cusps or folds in the lower molars. The spur in the slightly worn upper teeth figured by Young (1932a, pl. 7, figs. 6-9), however, is very clearly shown in the molars of four subadult skulls of *Moschus moschiferus* [A.M.N.H. (M.) Nos. 32251 and 85400-85402] as well as in the slightly worn premolars of adult skulls. In teeth worn to a greater extent (apparently used for comparison by Young) the spur is worn off. The development of the cingular cusps or folds in the lower molars, as judged from the figures (Young, 1932a, pl. 7, figs. 2-4), is not greater than in some of our specimens.

Consequently the fossil *Moschus* from Yenchingkou presents only very slight average

TABLE 44
MEASUREMENTS (IN MILLIMETERS) OF THE SKULL AND TEETH OF *Moschus moschiferus*

	Condylo- basal Length	Zygo- matic Width	Width Outside Molars	P ² -M ³ L	M ¹⁻³ L	P ₂ -M ₃ L	M ₁₋₃ L
<i>M. m. plicodon</i>							
A.M.N.H. Nos.							
18564 (type)	145e	62	46	43	26	—	33
18763	—	—	—	—	—	46e	30
18553b	—	—	—	—	—	48	31
18556	—	—	—	—	—	—	29
18566a	—	—	—	—	—	—	29
18566c	—	—	—	—	—	—	31
18577a	—	—	—	—	—	—	31
18580	—	—	—	—	26	—	—
<i>M. m. sifanicus</i>							
A.M.N.H.(M.) No.							
110500, ♀	143	61	45	41	23	43	28
<i>M. m. moschiferus</i>							
A.M.N.H.(M.) No.							
46405, ♂	142	64	45	42	25	46	29
<i>M. moschiferus</i>							
A.M.N.H.(M.) Nos.							
83995	144	62	45	42	25	48	30
69500	147	60	43	37	23	42	28
17951	—	65	46	41	25	45	28

differences from the recent musk deer. It is apparently not identical with the subspecies living today in the same region. Like the fossil *Moschus* from Choukoutien, the form from Yenchingkou has stronger cingular cusps or folds in the lower molars than the recent musk deer, and for this reason we consider it subspecifically distinct.

MUNTIACUS RAFINESQUE

Muntiacus RAFINESQUE, 1815, *Analyse de la nature*, p. 56.

GENERIC TYPE: *Cervus muntjak* Zimmermann.

DIAGNOSIS: Small deer with antlers in the male only, borne on long pedicles and having a main beam and a usually short brow tine; the pedicles are continued anteriorly as prominent converging ridges on the frontals; large depression on lacrimal; tusk-like upper canines in the male, turned outward at tip; P₄ of a "primitive" type (metaconid separated from paraconid).

Muntiacus muntjak margae Hooijer

Muntiacus muntjak margae HOOIJER, 1951, *Amer. Mus. Novitates*, no. 1495, pp. 4-11.

TYPE: A.M.N.H. No. 39166, right and left antlers and pedicles, probably associated and complete.

PARATYPES: A.M.N.H. Nos. 39165, right antler and portion of pedicle; 18682, mandibular rami, probably associated, with right P₄-M₃ and left P₂-M₃.

REFERRED SPECIMENS: A.M.N.H. Nos. 18684, left mandibular ramus with P₂₋₄; 18685, mandibular rami, probably associated, with right P₄-M₂ and left P₂-M₂; 18686, right mandibular ramus with P₃-M₃; 18818, mandibular rami, probably associated, with right P₂-M₃ and left P₃-M₁; 21793, left antler and portion of pedicle; 39154a, b, two mandibular rami; a, right P₃-M₃; b, left P₂-M₃; 39155a-c, three mandibular rami; a, left P₄-M₃; b, right P₄-M₃; c, right P₃-M₁; 39156, right mandibular ramus with P₃-M₃; 39157a, b, two mandibular rami; a, right P₃-M₃; b, left P₃-M₃; 39158, left mandibular ramus with P₂-M₁; 39159a, b, two mandibular rami; a, right P₄-M₂; b, left P₃-M₂; 39161, right antler; 39162, right antler; 39163, left antler and portion of pedicle; 39164, right antler and portion of pedicle.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Like modern *Muntiacus muntjak* (Zimmermann) but larger; antler rather short, and but slightly curved; brow tine small and close to the burr.

DISCUSSION

The antlers are quite typical of the genus *Muntiacus* (*Cervulus auct.*) but decidedly larger than those of recent *Muntiacus reevesi* (Ogilby) inhabiting a large part of China, including Szechwan.

On the other hand, the antlers do not differ much in size from those of larger modern forms of *Muntiacus*, e.g., *Muntiacus muntjak vaginalis* (Boddaert), which nowadays just reaches the southern border of China in Yunnan and Kwangsi (Allen, 1940, p. 1149). In the two complete Yenchingkou specimens the antler is shorter than the pedicle, while in recent *Muntiacus* the antler usually is longer than the pedicle.

The fossil antlers vary greatly in size; A.M.N.H. No. 39165 is particularly large. The antler is but slightly curved, and the brow tine is always close to the burr and is rather small.

There are also a number of jaw fragments with teeth referable to the muntjak. Without doubt there are more specimens in the Yenchingkou collection than those listed above. However, as shown by some incomplete skulls referred to below, the tufted deer, *Elaphodus*, also forms part of the Yenchingkou fauna. This animal is of about the same size as the Yenchingkou muntjak, and after comparison of the cheek teeth in series of skulls of both genera the only difference

we can find is in the last lower premolar, P_4 , and even this difference is not constant.

In *Muntiacus* the P_4 has as a rule the metaconid separated from the paraconid, leaving the trigonid open on the lingual side. In the *Elaphodus* P_4 the metaconid and paraconid are fused, and there is consequently a closed anterior fossette. In the P_4 of a female *Muntiacus muntjak vaginalis* from Yunnan [A.M.N.H. (M.) No. 43056] the paraconid and metaconid form a complete inner wall to the anterior fossette. There is no doubt that the mandible belongs to the skull, which with its heavy frontal ridges, comparatively small lacrimal fossa, and unexpanded upper end of the premaxillary in contact with the nasal¹ is correctly identified. The mandibular rami referred to the present form all possess a P_4 of the simple type commonly found in recent *Muntiacus*. There is a tendency for the anterior fossette to close; some fossil specimens (A.M.N.H. Nos. 39154 and 39155) have projections from both paraconid and metaconid constricting the entrance to the inner valley.²

¹ In the skull of *Muntiacus crinifrons* (Sclater) from Chekiang in the American Museum of Natural History [A.M.N.H. (M.) No. 56991, the third specimen known of this species], a narrow tongue of the maxillary separates the nasal from the premaxillary as in *M. reevesi*, a difference from *Muntiacus muntjak vaginalis* not noticed by Allen (1940, p. 1160).

² Teilhard de Chardin and Leroy (1942, p. 68) tentatively refer the material from Choukoutien identified as "*Hydropotes* sp." by Young (1932a, p. 22) to *Cervulus* (= *Muntiacus*), but these specimens have the P_4 with paraconid and metaconid fused as in recent *Hydropotes*. One mandible (Young, *ibid.*, p. 23, fig. 5a) differs from the others in the simpler shape of P_4 (metaconid not fused with paraconid), and this particular specimen might belong to *Muntiacus*.

TABLE 45
MEASUREMENTS (IN MILLIMETERS) OF ANTLERS AND PEDICLES OF
RECENT AND FOSSIL *Muntiacus*

	<i>M. reevesi</i>	<i>M. muntjak margae</i>
Length of pedicle, inner side	30-71	73a-78a
Anterior-posterior diameter of pedicle	13-18	17-30
Length of antler, in straight line, burr included	56-92	48+-93+
Height of fork above burr, burr included	8-20	14-26
Length of brow tine above burr, burr included	9-25	22-41

TABLE 46^a
MEASUREMENTS (IN MILLIMETERS) OF ANTLERS OF RECENT AND FOSSIL *Muntiacus*

	Length of Pedicle	Antero- posterior Diameter of Pedicle	Length of Antler	Height of Fork	Length of Brow Tine
<i>M. reevesi</i> A.M.N.H.(M.) 18 specimens	30-71	13-18	58-92	8-20	9-25
<i>M. m. margae</i> A.M.N.H. Nos.					
21793	—	20	—	26	41
39161	—	—	93+	17	—
39162	—	—	59	17	23
39163	—	17	48+	14	19+
39164	—	24	—	23	34+
39165	—	30	—	20	—
39166 (right)	78a	19	76	17	23
39166 (left)	73a	19	67	15	22
<i>M. m. vaginalis</i> A.M.N.H.(M.) 4 specimens	67-87	15-21	87-102	19	32
<i>M. crinifrons</i> A.M.N.H.(M.) 1 specimen	44	14	64	21	21
<i>M. kendagensis</i> After Stremme, 1911	34	25	115+	36	107
After von Koenigswald, 1933	—	28	183a	39	101
After von Koenigswald, 1933	84+	24	160a	24	92

^a This table is presented in more detail in Hooijer, 1951a (pp. 8-9).

Most of the fossil specimens from Yenchingkou are larger than *Muntiacus muntjak vaginalis*, the large Indian muntjak extending northward into China. The teeth of the muntjak from Yenchingkou are also larger than those of the recent *Muntiacus reevesi* inhabiting the same region, as shown in the following measurements (in millimeters):

	LENGTH P ₂ -M ₃	LENGTH M ₁ -M ₃
<i>Muntiacus reevesi</i>	49-61	31-38
<i>M. m. vaginalis</i>	63-74	37-44
Yenchingkou	70-86	40-50

Thus the fossil muntjak from Yenchingkou is characterized by its large size, like so many of the other elements of the fauna. The fossil forms of *Muntiacus* from China thus far described are not especially large. *Muntiacus bohlini* (Teilhard de Chardin, 1940, p. 79) from the Lower Pleistocene of Nihowan (Teilhard de Chardin and Piveteau, 1930, p. 44,

as *Cervulus cf. sinensis*¹) and from the Middle Pleistocene of Choukoutien, to which probably also belongs the left mandibular ramus figured as "*?Hydropotes* sp." by Young (1932a, p. 23, fig. 5a), fills the gap between *Muntiacus reevesi* and the Yenchingkou specimens as far as tooth size is concerned. The character that would distinguish *Muntiacus bohlini* is that the antler index stays between 45 and 50, which is a rather, but not impossibly, low figure for a recent muntjak. In *Muntiacus lacustris* (Teilhard de Chardin and Trasaert, 1937a, p. 21) from the Pliocene of Yushè, Shansi, the pedicle is again shorter, and the antler index is lower than 30. Teilhard de Chardin (1940, p. 85) concludes that, from the Pliocene upward, the muntjaks have acquired (relatively) longer pedicles. As stated above, the Yenchingkou muntjak

¹ The figure of the antler and pedicle given by these authors (*ibid.*, fig. 16) is two-thirds natural size and not natural size as stated in the legend to the figure.

TABLE 47^a
MEASUREMENTS (IN MILLIMETERS) OF TEETH OF RECENT AND FOSSIL *Muntiacus*

	P ₁ -M ₃	M ₁₋₃	P ² -M ³	M ¹⁻³
<i>M. reevesi</i>				
A.M.N.H.(M.)				
31 specimens	49-61	31-38	43-55	24-31
<i>M. m. vaginalis</i>				
A.M.N.H.(M.)				
7 specimens	63-74	37-44	58-68	32-39
<i>M. crinifrons</i>				
A.M.N.H.(M.)				
1 specimen	67	40	60	34
<i>M. m. margae</i>				
A.M.N.H. Nos.				
18682	86	50	—	—
18686	—	45	—	—
18818	83	—	—	—
39154b	78	46	—	—
39155a	—	48	—	—
39155b	—	42	—	—
39156	70	43	—	—
39157a	—	50	—	—
39157b	—	40	—	—

^a This table is presented in more detail in Hooijer, 1951a (pp. 9-10).

has a relatively long pedicle, or rather a short antler, but there is much variation in this character.

Muntiacus kendengensis (Stremme, 1911, p. 106, pl. 20, fig. 2) from the Pleistocene of Java is characterized mainly by the great length of its brow tine. Better specimens have been figured by von Koenigswald (1933, p. 59, pl. 19, figs. 1-2). Tokunaga and Takai (1939, p. 246) refer *M. kendengensis* to the genus *Metacervulus* Teilhard de Chardin and Trassaert (1937a, p. 13), which differs from *Muntiacus* in the presence of a second, posteriorly directed tine. However, the beam of Stremme's type specimen is not complete, and von Koenigswald's specimens do not show this second bifurcation at all. The measurements of the recent and fossil antlers and teeth of *Muntiacus* are given in tables 46 and 47.

The Yenchingkou muntjak, though far less distinctive than the fossil Javan *Muntiacus kendengensis* with its long brow tine, nevertheless might be given a special name on account of its large size. Its occurrence beyond the range of recent *Muntiacus muntjak* and within the region now roamed by

the smallest species, *Muntiacus reevesi*, gives this form additional interest. It is also larger than the other Chinese fossil muntjaks thus far described. We regard the Yenchingkou muntjak provisionally as a subspecies of *Muntiacus muntjak*. Better material of the skull might eventually prove that its affinities are rather with *Muntiacus reevesi* or *M. crinifrons*, but this must remain unsettled for the moment.

ELAPHODUS MILNE-EDWARDS

Elaphodus A. MILNE-EDWARDS, 1871, Bull. Nouv. Arch. Mus. Paris, vol. 7, p. 93.

GENERIC TYPE: *Elaphodus cephalophus* Milne-Edwards.

DIAGNOSIS: Like *Muntiacus*, but with very small antlers, no frontal ridges, premaxilla expanded posteriorly, male upper C not turned outward at tip, P₄ of the "advanced" type (metaconid fused with paraconid).

Elaphodus cephalophus megalodon Hooijer

Elaphodus cephalophus megalodon HOOIJER, 1951, Amer. Mus. Novitates, No. 1495, pp. 11-17.

TYPE: A.M.N.H. No. 18828, front of a female skull with right M¹⁻³ and left P², P⁴-M³.

TABLE 48
MEASUREMENTS (IN MILLIMETERS) OF SKULL AND TEETH OF FOSSIL
AND RECENT *Elaphodus cephalophus*

	Nasals, Greatest Width	Maxil- lary, Greatest Height	Lacrimal Fossa, Longer Diameter	Width Over Inner Borders of Infra- orbital Fora- mina	P ² -M ³ L	M ¹ -M ³ L	DM ²⁻⁴ L	P ₂ -M ₁ L	P ₄ -M ₂ L
<i>E. c. megalodon</i>									
A.M.N.H. Nos.									
18828, ♀	33	35	34	37	71	41	—	—	—
18829, ♂	29	33	27	—	—	—	35	—	—
18830	—	—	—	—	—	—	36	—	—
18831	—	—	—	—	—	—	34	—	—
18508	—	—	—	—	—	—	—	40	—
18837	—	—	—	—	—	—	—	43	—
39187	—	—	—	—	—	—	—	45	—
18832	—	—	—	—	—	—	—	—	36
18837	—	—	—	—	—	—	—	—	37
<i>E. c. cephalophus</i>									
After Milne-Edwards, ♂	—	33	35	—	62	37	—	39	34
A.M.N.H.(M.) No.									
43060, ♀	30	30	31	35	58	32	—	36	31
<i>E. c. ichangensis</i>									
A.M.N.H.(M.) Nos.									
84337, ♀	—	—	30	—	—	—	33	—	—
55983, ♂	23	31	33	31	—	34	29	—	—
<i>E. c. michianus</i>									
A.M.N.H.(M.) Nos.									
43043, ♂	25	29	32	34	55	32	—	35	31
84462, ♂	25	30	29	34	59	33	—	35	32
84463, ♂	27	31	33	34	59	34	—	37	32

PARATYPES: A.M.N.H. Nos. 18829, front of subadult male skull on the right side with C, DM²⁻⁴, M¹⁻²; 18508, right mandibular ramus with P₂-M₁.

REFERRED SPECIMENS: A.M.N.H. Nos. 18830, right maxilla with DM²⁻⁴, M¹⁻²; 18831, right maxilla with DM²⁻⁴; 18832, right mandibular ramus with P₄-M₂; 18833, right pedicle and antler; 18837, left mandibular ramus with P₄-M₂; 21786, crushed skull with right M¹⁻³ and left DM⁴, M¹⁻³; 39186, left pedicle; 39187, left mandibular ramus with P₂-M₁.

HORIZON AND LOCALITY: Pleistocene; Yen-chingkou, Szechwan, China.

DIAGNOSIS: Like modern *Elaphodus cephalophus* Milne-Edwards but larger; nasals broad and less compressed posteriorly than in the recent forms; lacrimal fossa large, its long axis set obliquely to that of the orbit; teeth

relatively, as well as absolutely, larger than the recent form.

DISCUSSION

The present fossil material is the first to be recorded indicating the presence of the tufted deer, *Elaphodus*, in the Pleistocene fauna of China. The recent species is confined to China and has been divided into several subspecies.

The cranial differences between the Chinese races accepted by Allen (1940, p. 1143) are very slight. *Elaphodus cephalophus ichangensis*, within the range of which the fossil material was found, differs from the typical subspecies (which is confined to the highlands of southwestern China) in its smaller size, relatively shorter nasals, and in the shape of the lacrimal fossa which is more regularly oval, smaller, and deeper than in *E. c. cephalophus* and has the long axis set

more obliquely to that of the orbit. *Elaphodus cephalophus michianus*, the range of which lies between that of *E. c. ichangensis* and the coast, is also smaller than the typical race, and the lacrimal fossa has its long axis not far removed from that of the orbit (Lydekker, 1915, pp. 34-39). Allen (1940, p. 1143) adds that in *E. c. michianus* the nasals are narrower and more compressed posteriorly than in *E. c. ichangensis*.

The adult fossil skull (A.M.N.H. No. 18828) is nearest in size to that of *E. c. cephalophus*, and the lacrimal fossa is large and irregularly oval. Its long axis, however, is set very obliquely as in *E. c. ichangensis*. The nasals are broader and less compressed than those in any of the recent skulls. The small canine alveoli just visible in front (the premaxillaries are lost) indicate that the skull belonged to a female.

The subadult skull (A.M.N.H. No. 18829) has a decidedly smaller lacrimal fossa, with its long axis less oblique than that in the adult fossil skull, apparently an age difference only. It belonged to a male.

The crushed skull (A.M.N.H. No. 21786) is inadequate for comparison, but the lacrimal fossa seems to be as large as that in A.M.N.H. No. 18828.

In the size of the teeth, the fossil tufted deer considerably exceeds the recent. The teeth are decidedly larger relative to the size of the skull in the fossil *Elaphodus* than in the recent deer. The mandibular rami, all with the P_4 showing the fusion of metaconid and paraconid, likewise exceed recent forms in the size of the teeth. The male skull of *E. c. cephalophus* figured by Milne-Edwards (1868-1874, pl. 67) exceeds the recent skulls we had at our disposal in size but is still inferior in dimensions, especially as regards the teeth, to the Yenchingkou material.

The single pedicle and antler referable to the present form (A.M.N.H. No. 18833) are larger than in any of the recent skulls. As compared with that figured by Milne-Edwards (*loc. cit.*), the fossil pedicle is shorter (24 mm. against 26 mm.), but the antler is longer (19 mm. as opposed to 16 mm.) and the pedicle is somewhat stronger (diameter 10 mm. against 8 mm.). In a fossil pedicle (A.M.N.H. No. 39186) only 16 mm. long, the diameter is 9 mm.; in available re-

cent skulls it is 7 mm. at the most.

The recent material for comparison is rather scanty; nevertheless it seems justifiable to recognize a separate subspecies among the Yenchingkou fossils. They give evidence of the diminution in size which this species has undergone in the course of the Quaternary. No fossil remains of *Elaphodus* have been previously recorded, and the only reference to this genus in the literature on the fossil mammals of China is a remark by Teilhard de Chardin and Trassaert (1937a, p. 29) that *Elaphodus* might be a last representative of *Paracervulus*. *Paracervulus* is a genus created by Teilhard de Chardin and Trassaert (*ibid.*, p. 15) for the inclusion of a number of antlers from the Pliocene of Yushè, Shansi. The genus is defined as a "Cervulinae" with a brow tine in high position, antlers slightly curved backward and inward, and pedicles continued forward as a ridge on the frontal. Four species are proposed, whereby specific value is attached to differences in the position and degree of reduction of the brow tine. The species *Paracervulus simplex*, characterized by the reduction of the brow tine to a swelling along the lower third of the antler, is stated (*ibid.*, p. 21) to be probably related to *Elaphodus*. The difference is that in *P. simplex* the pedicle is relatively shorter, being only about one-fourth as long as the antler, while in *Elaphodus* pedicle and antler are approximately of the same length. The difference is considered to be an "adaptive" one, the increase in length of the pedicle in the Muntiacini being seemingly a general fact.

If *Elaphodus* evolved from a form with *Paracervulus simplex*-like antlers and pedicles, a reduction of the antler is involved rather than an increase in length of the pedicle; the antlers in the Pliocene form are about five times as long as those in *Elaphodus*, while the pedicles in the Pliocene form are only one-third shorter and one-half greater in diameter, approximately, than in the recent form. The fossil pedicles from Yenchingkou are somewhat stronger but shorter than the recent; the material does not, however, permit conclusions as to evolutionary trends in the antlers of *Elaphodus*.

Tokunaga and Takai (1939, p. 245) regard the antlers on which the genus *Paracervulus* was based as young specimens of *Metacervu-*

lus, and Simpson (1945, p. 153) also includes *Paracervulus* in the genus *Metacervulus*. If this be adopted, it is hardly possible to assume a direct phylogenetic relationship between the Muntiacini of the Pliocene of Yushê and the Pleistocene and recent genus *Elaphodus*.

BOVIDAE

BUBALUS SMITH

Bubalus C. H. SMITH, 1827, in Griffith, The animal kingdom . . . by . . . Cuvier, vol. 5, pp. 371-373.

GENERIC TYPE: *Bos bubalis* Linnaeus.

DIAGNOSIS: Horn cores more or less triangular in cross section, curving downward and backward and well separated at base; frontal region convex anteroposteriorly; facial region elongated and slender; horn cores not far behind orbits; occiput rather low; palate much extended behind the last molars; the vomer fused with palatines; premaxillae in contact with nasals; P_2 not reduced in size.

Bubalus bubalis (Linnaeus)

Bos bubalis LINNAEUS, 1758, *Systema naturae*, ed. 10, vol. 1, p. 72.

Bibos geron MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 594-596 (in part).

REFERRED SPECIMENS: A.M.N.H. Nos. 18481, right horn core; 18484, posterior part of skull with base of right horn core; 18500, skull fragment with right M^3 and left P^4-M^3 ; 18503a, base of left horn core; 18504, partial skull with base of right horn core and right M^{1-3} ; 39193, right mandibular ramus with P_2-M_1 (broken); 21784, crushed skull, horn cores and premaxillae broken off, frontals and occiput damaged, and lower jaw, associated, with P^2-M^3 , and P_3-M_3 . C.N.H.M. No. P.14152, palate with right and left P^2-M^3 .

The reference of the following metapodials to the present species is provisional: A.M.N.H. Nos. 39206, left metacarpal; 39208, two left metacarpals; 39209, one right and one left metacarpal, probably associated; 18485, one left metacarpal and one left metatarsal; 39205, right metatarsal; 39207, right metatarsal.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Horn cores triangular in cross section, widely separated at base; profile of head straight; convexity of forehead moderate.

DISCUSSION

At Yenchingkou Granger collected a series of partial skulls, upper and lower jaws with teeth, and parts of the skeleton of a large bovid which were all recorded as *Bibos geron* (Matthew and Granger, 1923, p. 594). Matthew and Granger note that, although there is a considerable amount of variation in tooth pattern, among the skulls and horn cores there is no evidence of any true bovine type other than *Bibos*. They found, however, two distinct types of Bovinae represented in the foot material, differing in metapodial length (*ibid.*, p. 596). No identification of the second type of metapodials is given.

It seems very probable that Granger afterward had identified the second large bovid as *Bubalus*, for in Young (1936, p. 511) we read: "Remains of water-buffalo (not yet described) had been already collected at Yenchingkou by Dr. Granger (personal communication), but not preserved horn core." It was Young (1936, p. 511) who first placed *Bubalus* remains from Szechwan on record, viz., a horn core in association with jaws, teeth, and limb bones collected about 30 li¹ south of Yenchingkou. The specimen is tentatively referred to *Bubalus brevicornis* Young, a large, short-horned, massive-skulled water buffalo from the Pleistocene of Honan, Shansi, and Shantung. The horn core is re-described in a subsequent paper (Young, 1939, p. 322).

Thus while the water buffalo is already on record from the Pleistocene of Szechwan, it was thought to be absent among the skull materials in our collection from Yenchingkou, even though some metapodials in this collection might represent this form.

In our study of the bovine material of the Yenchingkou collection, however, it has become apparent to us that *Bubalus* is also represented in the cranial material. While some of the best-preserved skulls in the collection do have the high, arched, upwardly curved intercornual ridge at the vertex, as well as other characters that show that they

¹ One mile equals 2.78 li.

belong to the gaur (*Bibos gaurus*), there are a number of skulls and horn cores that cannot possibly have belonged to the gaur but do belong to *Bubalus*, the water buffalo. These specimens are listed above.

Two skulls (A.M.N.H. Nos. 18484 and 18504), although very incomplete, both have the base of the right horn core preserved, and this core is distinctly triangular in cross section. The upper surface is the widest of the three, and the vertical anterior surface is the narrowest. Both specimens are somewhat crushed above, especially No. 18484, while in No. 18504 the horn core stump is thrust out of its natural downward direction and now points upward. Even so, it is quite clear that the heavy intercornual ridge typical of the gaur is absent. The parietals above the linea nuchae superior are tilted forward relative to the occipital plane, and, with the frontals, they form a smoothly curved surface over the vertex of the skull which thus is very much less elevated than in a typical gaur. The frontals are convex from front to back, and the orbits are quite close to the horn cores; the distance from their posterior rims to the base of the cores is about equal to their diameters.

While A.M.N.H. No. 18484 is broken off at the level of the anterior border of the orbit, No. 18504 has the posterior part of the nasals preserved, and also a great portion of the right maxilla with three molars *in situ*. In the elongated form of the skull base the fossil again agrees very well with *Bubalus*.

The vomer, although damaged, is a quite prominent ridge in front of the basilar tubercles, and in A.M.N.H. No. 18504 it is seen to unite with the palatine bones. This is a condition typical for *Bubalus* and absent in *Bibos*, a most important distinguishing character that has enabled us to identify several more specimens as belonging to *Bubalus*, such as the crushed skull (A.M.N.H. No. 21786), the skull fragment (A.M.N.H. No. 18500), and the palate now in the Chicago Natural History Museum (C.N.H.M. No. P.14152).

Some isolated horn cores, because of their triangular cross section, belong under this heading. The base of a left horn core (A.M.N.H. No. 18503a) may even have belonged to skull A.M.N.H. No. 18504, while

a right horn core (A.M.N.H. No. 18481), with part of the skull still attached to it and broken off 19 cm. from its base, shows the triangular shape and the downward and backward curve very nicely. The measurements of the above-mentioned skulls and horn cores are given in table 49.

It will be observed that in general there is no appreciable difference in size between the recent and the fossil *Bubalus*, while in every aspect the fossil skulls agree closely with those of recent *Bubalus bubalis*. None of the horn cores in the American Museum collection is complete enough to determine whether or not they are as short as those of Young's *Bubalus brevicornis*; the measurements of Young's Szechwan specimen tentatively referred to this species are given in table 49 and show that the dimensions are similar to those of the recent and the Yenchingkou specimens.

The crushed skull A.M.N.H. No. 21784, which in the union of the vomer and palate shows that it belongs to *Bubalus*, also has the elongated skull base (length from basion to lateral postpalatal notches) typical of the water buffalo, while the median posterior border of the palate is about 40 mm. behind the level of the lateral postpalatal notches. The same condition is seen in skulls A.M.N.H. No. 18500 and 18504 and in the palate of C.N.H.M. No. P.14152. In the gaur the distance from basion to the lateral postpalatal notches is shorter, and the palate extends only about half as far behind these notches (about 20 to 25 mm. against 50 mm. in the recent water buffalo).

Skull A.M.N.H. No. 21784 fortunately is associated with the mandible, complete up to the front (the incisors are lost except for the left I_3 , but all alveoli are shown). In keeping with the elongated muzzle, the diastemal part of the mandible of the water buffalo is longer than that of the gaur. This *Bubalus* character shows up, again, in the fossil mandible; its length from front to P_2 is 185 mm.; in two recent water buffalo mandibles this is 175–180 mm., while in *Bibos gaurus* it is less.

We have to deal now with the dentition, which is beautifully preserved in skull A.M.N.H. No. 21784 as well as in the palate (C.N.H.M. No. P.14152), while the mandibu-

TABLE 49
MEASUREMENTS (IN MILLIMETERS) OF THE SKULL OF RECENT AND
FOSSIL *Bubalus bubalis*

	A.M.N.H.(M.) No. 54765	A.M.N.H.(M.) No. 54766	A.M.N.H.(M.)	A.M.N.H.(M.)	A.M.N.H. No. 18484 Yenchingku	A.M.N.H. No. 18504 Yenchingku	A.M.N.H. No. 21784 Yenchingku	A.M.N.H. No. 18503a Yenchingku	A.M.N.H. No. 18481 Yenchingku	Yenchingku, Young, 1939
Length from posterior end of nasals to vertex (opisthocranium)	225	205	225	215	—	225	—	—	—	—
Length from basion to lateral post-palatal notches	220	205	200	200	—	205	220	—	—	—
Length from posterior border of orbit to posterior base of horn core	215	175	180	175	200	200	—	—	—	—
Width of occipital condyles	115	125	120	130	125	130	130	—	—	—
Width of occiput over paramastoid processes	220	220	200	200	225	225	230	—	—	—
Least width of occiput between temporal fossae	145	110	115	130	100	115	120	—	—	—
Width of frontals at post-orbital constriction	230	220	230	220	250	240	—	—	—	—
Distance between orbit and anterior base of horn core	60	75	65	65	55	70	—	—	—	—
Diameter of orbit	65	70	70	65	—	65	—	—	—	—
Height of occiput from basion to external occipital protuberance	120	130	125	125	150	130	145	—	—	—
Height from basion to vertex	210	185	185	205	225a	215	—	—	—	—
Height from palatines to nasal	160	155	165	150	—	155	—	—	—	—
Diameters of horn core at base										
Upper surface	155	100	115	120	155	135	—	130	85	123
Anterior surface	90	65	60	70	95	90	—	90	70	68
Lower surface	135	95	110	110	125	115	—	110	75	107

lar dentition of A.M.N.H. No. 21784 is also perfect except for the P_2 , which is broken off. Is it possible to distinguish between the teeth of *Bibos gaurus* and *Bubalus bubalis*?

In a comparison between series of adult dentitions of *Bibos gaurus* and *Bubalus bubalis* one difference strikes the eye: in the gaur the anterior lower premolar, P_2 , is more reduced in size than in the water buffalo, and more simply built. It is very hard, however, to find further distinguishing dental characters. There is no difference in size, and the configurations of the enamel of premolars and molars, constantly changing through wear, do not show reliable specific characters either.

Rütimeyer (1866, p. 101) has remarked that in *Bubalus* the upper molars have the accessory columns less well developed than in *Bibos*. Koken (1870, pp. 64, 67, pl. 2) refers the quadrangularly shaped molar crowns to *Bibos* and the more anteroposteriorly elongated ones to *Bubalus*, but, as Stremme (1911, p. 128) remarks, this is largely a matter of different stages of wear and thus of a difference in age only. The crowns of the upper molars (as well as those of the lower molars) increase in transverse diameter but decrease in anteroposterior diameter towards the root, and no reliance can thus be placed on this sort of difference.

This is well illustrated by measurements

taken on unworn or hardly worn isolated molars, from specimens in A.M.N.H. No. 39200, close to the apex of the crown, at the middle of the height, and near the base of the crown, respectively:

	UPPER MOLAR	LOWER MOLAR
Anteroposterior		
Crown	36	36.5
Middle	32	32
Base	29	28
Transverse		
Crown	22	14
Middle	26	18
Base	29	22

On these teeth there are differences in diameter as great as 7 to 8.5 mm. between the base and the top of the crown. Measurements of the molar crowns thus must be used with great caution in comparative studies. Added

to that, the variable amount of cement coating the sides of the crown adds to the unreliability of the figures for crown measurements.

The accessory column in the upper molars, occasionally only a single spur, most often is a bilobed projection between protocone and hypocone, sometimes extending lingually beyond these. It is usually attached to the protocone in its basal part, while the apex is free to a variable height. Comparison between dentitions of approximately the same stage of wear does not show the gaur molars to have more developed accessory columns than those of the water buffalo.

In the lower molars, where the accessory column is on the outer surface between protoconid and hypoconid, there is no difference in development between the two species. In M_3 of the gaur there is also a small accessory column between hypoconid and talonid (hypoconulid), but it may be absent, and it

TABLE 50
MEASUREMENTS (IN MILLIMETERS) OF THE UPPER TEETH OF
Bubalus bubalis AND *Bibos gaurus*

	<i>Bubalus bubalis</i>				<i>Bibos gaurus</i>			
	A.M.N.H.(M.) No. 54765, Recent	A.M.N.H.(M.) No. 54766, Recent	A.M.N.H. No. 21784, Fossil	C.N.H.M. No. P.14152, Fossil	A.M.N.H.(M.) No. 54470, Recent	A.M.N.H.(M.) No. 113758, Recent	A.M.N.H. No. 18465, Fossil	A.M.N.H. No. 39188, Fossil
P ²								
L	18	22	16	18	18	23	21	20
W	15	18	16	15	15	17	17	—
P ³								
L	19	23	21	19	18	21	22	—
W	20	24	21	21	18	23	21	18
P ⁴								
L	18	20	19	18	17	20	22	—
W	22	25	23	23	21	24	22	—
M ¹								
L	27	31	31	26	24	28	29	—
W	25	29	28	28	26	28	28	30
M ²								
L	31	34	35	31	27	30	32	27
W	27	28	28	29	25	29	28	31
M ³								
L	35	36	36	37	30	34	34	33
W	26	28	28	26	24	29	27	30
P ² -M ³								
L	153	164	160	152	138	158	164	147

TABLE 51

MEASUREMENTS (IN MILLIMETERS) OF THE LOWER TEETH OF
Bubalus bubalis AND *Bibos gaurus*

	<i>Bubalus bubalis</i>				<i>Bibos gaurus</i>			
	A.M.N.H.(M.) No. 54765, Recent	A.M.N.H.(M.) No. 54766, Recent	A.M.N.H. No. 21784, Fossil	A.M.N.H. No. 39193, Fossil	A.M.N.H.(M.) No. 54470, Recent	A.M.N.H.(M.) No. 113746, Recent	A.M.N.H. No. 18465, Fossil	A.M.N.H. No. 39188, Fossil
P ₂								
L	17	19	—	19	13	13	16	15
W	11	13	—	12	10	10	12	11
P ₃								
L	22	23	22	23	19	19	25	22
W	14	15	13	15	13	13	15	14
P ₄								
L	24	25	23	25	21	21	26	24
W	16	18	15	16	15	15	16	16
M ₁								
L	26	31	29	—	25	24	29	25
W	18	19	20	—	18	18	20	21
M ₂								
L	31	34	33	—	28	27	31	29
W	19	19	20	—	19	20	21	23
M ₃								
L	44	48	46	—	40	38	45	45
W	18	20	20	—	19	19	20	22
P ₂ -M ₃								
L	165	177	178	—	147	142	172	157

is not developed in the water buffalo.

In P₃ and P₄ there seems to be a somewhat greater tendency in the water buffalo for the posterior inner valley to form an isolated fossette with prolonged wear than in the gaur, in which latter form the posterior inner valley is more often a shelving notch that does not form an isolated enamel lake with wear. But the most important differential character is the larger size of P₂ in the water buffalo as compared with the gaur, as already mentioned.

Of the mandible fragments in the Yenchingkou collection, only one can be identified as *Bubalus bubalis*, A.M.N.H. No. 39193. The difference in size of the anterior premolar between the water buffalo and the gaur is shown in table 51, in which the measurements of the dentition of the two best-preserved fossil skulls of *Bibos gaurus* are presented.

It was in the metapodials that Matthew and Granger (1923, p. 596) found evidence of the coexistence of two large bovids in the Yenchingkou collection, "one with extremely short metapodials, the other of larger size and with metapodials somewhat longer than in the American bison" (*loc. cit.*). There is a very marked size difference indeed, both in the metacarpal and in the metatarsal. Four of the 10 isolated specimens of the metacarpal and five of the eight isolated metatarsals we can safely refer to the gaur, and these are considered below under that head. The remaining specimens, however, although they resemble *Bubalus* in their shortness and considerable expansion at the distal end, are not quite so long as their homologues in recent *Bubalus bubalis*.

It will be seen from table 52 that the distal expansion of the Pleistocene Yenchingkou metacarpals is the same as in recent *Bubalus*

TABLE 52
MEASUREMENTS (IN MILLIMETERS) OF THE METACARPALS IN VARIOUS *Bubalus* SPECIES

	Length	Proximal Width	Middle Width	Distal Width	Ratio: Distal Width/Length
<i>B. bubalis</i>					
A.M.N.H.(M.) Nos.					
54765	237	83	57	92	0.39
54766	230	76	51	86	0.37
Yenchingkou					
A.M.N.H. Nos.					
39208	215	87	60	95a	0.44a
39208	210	91	62	97	0.46
18485	202	76	52	84	0.42
39206	194	78	53	87	0.45
39209	189	77	52	86	0.46
39209	186	—	51	85a	0.46a
<i>B. teilhardi</i>					
Young, 1932a (large)	295	91	53	91	0.31
Young, 1932a (small)	260	79	46	86	0.33
Zdansky, 1928	259	89	56.5	91.5	0.35
A.M.N.H. No. 26307	273	85	50.5	—	—
<i>B. wansjocki</i>					
Boule and Teilhard de Chardin, 1928	210	90	70	100	0.47
<i>B. mephistopheles</i>					
Teilhard de Chardin and Young, 1936	205	72-79	50-59	86-90	—

TABLE 53
MEASUREMENTS (IN MILLIMETERS) OF THE METATARSALS IN VARIOUS *Bubalus* SPECIES

	Length	Proximal Width	Middle Width	Distal Width	Ratio: Distal Width/Length
<i>B. bubalis</i>					
A.M.N.H.(M.) Nos.					
54765	265	68	48	83	0.31
54766	260	67	45	82	0.32
Yenchingkou					
A.M.N.H. Nos.					
18485	226	72	50	87	0.38
39205	224	69	48	83	0.37
39207	213	64	46	81	0.38
<i>B. teilhardi</i>					
Young, 1932a	290	73	46.5	81	0.28
<i>B. wansjocki</i>					
Boule and Teilhard de Chardin, 1928	250	75	56	85	0.34
<i>B. mephistopheles</i>					
Teilhard de Chardin and Young, 1936	230	60	42	60	0.26

bubalis. In length our specimens are more like their homologues in some fossil northern Chinese species such as *Bubalus wansjocki* Boule and Teilhard de Chardin from the Upper Pleistocene of Sjara-osso-gol in Shensi, also reported from Manchuria, and *Bubalus mephistopheles* Hopwood from Anyang in Honan. Unfortunately, the metapodials of *Bubalus brevicornis* Young (1936) from the Pleistocene of Honan, to which the horn core from Szechwan described by Young was provisionally referred, have not been described. The metacarpals of *Bubalus teilhardi* Young from Choukoutien fall into two size groups, but they are much longer than our fossils from Yenchingkou and in recent *Bubalus bubalis*, and also relatively less expanded distally.

In the metatarsals, too, the fossil *Bubalus* from Yenchingkou differs from the living water buffalo (table 53). The fossil bones are shorter than the recent, as are those in *Bubalus wansjocki* and *Bubalus mephistopheles*, while the metatarsals of *Bubalus teilhardi* are, again, much longer and less expanded at the distal end; the last condition also holds for *Bubalus mephistopheles*.

Thus while the skull remains from Yenchingkou described above suggest not another water buffalo but the living *Bubalus bubalis*, the metapodials are rather short when compared with those of the recent form, at least as far as our material for comparison goes. In dimensions the fossil *Bubalus* metapodials from Yenchingkou were found to resemble some extinct northern Chinese forms, notably *Bubalus wansjocki* from Sjara-osso-gol.

If the metapodials do not belong to the same species as the skull remains, the presence of a third large bovid at Yenchingkou must be accepted. Although the difference between the recent and the fossil metapodials is now striking, it may become less pronounced if more intergrading specimens are found. Between the recent and the fossil skulls there seems to be no more than a subspecific difference, and the difference now found in the metapodials also may be a matter of subspecific differentiation only. Until more material is examined, the metapodials are here provisionally referred to *Bubalus bubalis* (Linnaeus).

BIBOS HODGSON

Bibos HODGSON, 1837, Jour. Asiatic Soc. Bengal, vol. 6, p. 499.

GENERIC TYPE: *Bibos subhemachalus* Hodgson.

DIAGNOSIS: Horn cores more or less elliptical in cross section, curving outward and upward; frontal flat or concave; face shortened; occiput high; palatines not fused with the vomer; premaxillae not in contact with nasals; P_2 reduced in size.

Bibos gaurus grangeri, new subspecies

Bibos geron MATTHEW AND GRANGER, 1923, Bull. Amer. Mus. Nat. Hist., vol. 48, pp. 594-596 (in part).

TYPE: A.M.N.H. No. 18465, skull, with left horn core, premaxillae, and tip of nasals missing but restored, mandible, and most of the postcranial skeleton.

PARATYPE: A.M.N.H. No. 39188, skull with right horn core almost complete, palate and premaxillae missing but right P_2-M^3 present, and right and left mandibular ramus, associated, with right P_2-M_3 , and left P_4-M_3 .

REFERRED SPECIMENS: A.M.N.H. Nos. 39215, right mandibular ramus with P_2-M_3 ; 18497, right horn core; 21782, back of skull with right horn core; 39177, right mandibular ramus with P_2-M_3 ; 39178, two maxilla fragments with right P^4-M^3 and left M^{1-3} , three fragments of a mandible with right P_2-M_3 and left P_{2-4} , most probably associated; 39189, right mandibular ramus with P_2-M_3 ; 39190, left mandibular ramus with P_2-M_3 ; 39191, right mandibular ramus with P_2-M_1 ; 39192, two left mandibular rami with P_2-M_2 ; 39211, one right and one left metacarpal, probably associated; 39212, one left and one right metacarpal, not associated; 39210, two left metatarsals; 39213, one left and one right metatarsal, not associated; 39214, right metatarsal.

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Like modern *Bibos gaurus* (C.H. Smith) but larger.

DISCUSSION

For the first record of *Bibos* teeth from China we must go back to Koken (1885, p. 64), who described several upper molars and

TABLE 54

MEASUREMENTS (IN MILLIMETERS) OF THE SKULL OF RECENT AND FOSSIL *Bibos gaurus*

	<i>B. gaurus</i>						<i>B. g. grangeri</i>			
	A.M.N.H. (M.) No. 54468	A.M.N.H. (M.) No. 54470	A.M.N.H. (M.) No. 87621	A.M.N.H. (M.) No. 112979	A.M.N.H. (M.) No. 113758	A.M.N.H. (M.) No. 139690	A.M.N.H. No. 18465	A.M.N.H. No. 39188	A.M.N.H. No. 21782	A.M.N.H. No. 18497
Length from posterior end of nasals to vertex (opisthocranium)	250	275	235	240	265	220	285	275	—	—
Length from basion to lateral post-palatal notches	185	185	185	180	180	—	205	—	—	—
Length from posterior border of orbit to posterior base of horn core	225	215	180	210	220	220	235	225	—	—
Width of occipital condyles	125	110	115	115	135	—	130	140	120	—
Width of occiput over paramastoid processes	205	200	185	190	225	—	230	220	215	—
Least width of occiput between temporal fossae	140	120	90	135	95	105	100	115	145	—
Width of frontals at postorbital constriction	250	235	225	250	235	240	260	270	—	—
Distance between orbit and anterior base of horn core	110	105	100	115	110	105	110	85	—	—
Diameter of orbit	60	65	70	60	65	65	65	70	—	—
Height of occiput from basion to external occipital protuberance	130	120	125	120	140	—	135	145	140	—
Height from basion to vertex	285	275	245	270	255	—	260	310	260	—
Height from palatines to nasal	165	170	165	165	180	185	200	—	—	—
Diameters of horn core at base										
Antero-posterior	135	135	100	130	125	145	130	130	140	140
Vertical	100	90	75	95	90	95	100	95	95	95

one lower molar. Schlosser (1903, pp. 158-159) mentions both *Bibos gaurus* and *Bibos* sp., the former said to have come from Honan.

When Matsumoto (1915, p. 21) created a new fossil species, *Bibos geron*, on material from Szechwan, he had available only a left maxillary fragment with M^3 , and a left ramus of the mandible with P_4-M_3 .

All the large bovine material collected by Granger at Yenchingkou was referred in the preliminary paper of 1923 by Matthew and Granger to *Bibos geron*. The skull A.M.N.H. No. 18465 was selected as neotype for this species, but the specimen was figured (Matthew and Granger, 1923, figs. 26, 27) as *Bibos ? geron*. There was enough postcranial

material available from the same pit to make a mounted skeleton, which is now on exhibit in the American Museum of Natural History (pl. 37). Before the skeleton was mounted, measurements of various bones were taken by Robert G. Chaffee, and these are recorded in table 55. Granger (1938) has devoted a popular article to this skeleton.

Following Matthew and Granger's record of *Bibos geron* from Wanhhsien, Young (1939, p. 323) also mentions *Bibos geron* from the same province on the evidence of horn cores. With a view to the presence at the same locality of an equally large *Bubalus*, a number of upper and lower jaws were left unidentified.

As we state above under the heading

TABLE 55

MEASUREMENTS (IN MILLIMETERS) OF THE SKELETON OF A RECENT AND A FOSSIL *Bibos gaurus*
(Taken by Dr. R. G. Chaffee.)

	<i>B. gaurus</i> A.M.N.H.(M.) No. 112979	<i>B. gaurus grangeri</i> A.M.N.H. No. 18465
Vertebrae		
Atlas		
Length	85	107
Width	207	253
Axis		
Length	103	99
Width	108	84
Cervical 6		
Length of centrum	81	75
Width of centrum (posterior)	60	69
Height of spine	99	139a
Dorsal 1		
Length of centrum	71	79
Width of centrum	60	72
Height of spine	327	412a
Dorsal 6		
Length of centrum	69	75a
Width of centrum	42	53
Height of spine	371	384a
Dorsal 11		
Length of centrum	67	66a
Width of centrum	38	46
Height of spine	273	275a
Lumbar 1		
Length of centrum	71	75a
Width of centrum (anterior)	51	58a
Height of spine	135	132a
Lumbar 4		
Length of centrum	76	81
Width of centrum	54	64
Height of spine	104	111a
Sacrum		
Length	226	244a
Width	222	240a
Length of cervicals, extended	580	636a
Length of dorsals, extended	860	875a
Length of lumbar, extended	445	462a
Length of caudals, extended	735	817a
Fore limb		
Height of scapula	465	586a
Humerus		
Total length	383	471a
Articular length	325	367
Radius-ulna		
Total length	461	558
Articular length	319	420
Fore foot, total length, extended, without hoof	396	490
Hind limb		
Pelvis		
Total length	530	689a

TABLE 55—(continued)

	<i>B. gaurus</i> A.M.N.H.(M.) No.112979	<i>B. gaurus grangeri</i> A.M.N.H. No. 18465
Width of ilia	482	546a
Width at upper border of acetabulum	268	329a
Femur		
Total length	468	553a
Articular length	436	519a
Tibia-fibula		
Total length	439	536
Articular length	392	474
Hind foot, total length, extended, without hoof	573	696a
Articular length	471	585a
Height at shoulder, standing	1580	1880a

Bubalus bubalis it is practically impossible to distinguish between the premolars and molars of *Bibos gaurus* and *Bubalus bubalis*; only the P_2 is consistently smaller in the gaur than in the water buffalo. This tooth, however, was not present in the material on which Matsumoto (1915) based his new species *Bibos geron*. The teeth are very well figured in Matsumoto's report (1915, pl. 9, figs. 1-3; pl. 10, figs. 1-3), and indeed there is nothing in them that proves their distinctness. The measurements of the teeth given by Matsumoto (p. 21) show that they are of the same size as those of *Bubalus bubalis* and *Bibos gaurus* (our tables 50, 51). Consequently, *Bibos geron* Matsumoto is a name based on some fossil teeth that may have belonged either to *Bubalus bubalis* or to *Bibos gaurus*.

In 1928 Zdansky recorded *Bibos geron* from Choukoutien on the evidence of isolated teeth, a crushed horn core, and limb bones including metatarsals. However, according to Young (1932a, p. 78) this material is *Bubalus teilhardi*, as proved by the subsequent discovery of better skull remains. For a description of the dentition reference is made to Zdansky (1928); the horn core described as *Bibos geron* by this author appears to belong to *Ovis ammon* (Young, 1932a, p. 74). The American Museum of Natural History has an exchange collection of Choukoutien fossils from Uppsala, and in this collection are some molars and postcranial material under the name *Bibos geron*. A metacarpal (A.M.N.H. No. 26307) falls within the limits of *Bubalus teilhardi* as given by Young (1932a, p. 88), and its measurements are recorded in table

52 under that species. It will be observed that these Choukoutien metacarpals are more expanded at the distal end than those of *Bibos gaurus*.

The skull A.M.N.H. No. 18465 in the Yenchingkou collection is a perfect specimen of a large *Bibos gaurus*; it is illustrated as it is now restored in plates 33-35. The dentition is perfectly preserved as far as the premolars and molars go; the incisors are restorations. The relation between the vomer and the palatines cannot be studied in this specimen, but enough characters remain to show that this is a gaur skull. The elliptical cross section of the right horn core at the base (the left horn core is restored), the great prominence of the intercornual ridge, the concavity of the frontals from front to back, the great distance between the orbit and the base of the horn core, and the relative smallness of the anterior lower premolar are points in which the specimen differs from *Bubalus*. The second best *Bibos gaurus* skull in the Yenchingkou collection (A.M.N.H. No. 39188) is that of an older animal, as shown by its more worn teeth, and in some dimensions it is even larger than No. 18465, notably in the height of the occiput on which the intercornual ridge is a very high, arched ridge with excrescences, as is common in old animals. No palatines and only a very small part of the vomer is preserved. Most of the two rami of the mandible are present; as can be seen from table 51 the P_2 is even slightly smaller than that in A.M.N.H. No. 18465. The tooth rows are decidedly shorter in the present specimen than in A.M.N.H. No. 18465, but

TABLE 56

MEASUREMENTS (IN MILLIMETERS) OF THE METACARPALS IN RECENT AND FOSSIL *Bibos gaurus*

	Length	Proximal Width	Middle Width	Distal Width	Ratio: Distal Width/Length
<i>B. gaurus</i>					
A.M.N.H.(M.) Nos.					
112979	250	69	46	67	0.27
54470	240	77	46	73	0.30
<i>B. g. grangeri</i>					
A.M.N.H. Nos.					
39211	289	94	56	86	0.30
39211	287	89	55	84	0.29
39212	283	—	53	90	0.32
39212	281	72	43	71	0.25

this is only because the individual elements have lost much of their length through wear and are now close together with their less anteroposteriorly elongated bases.

The measurements of the Yenckingkou skulls are given with those of recent *Bibos gaurus* skulls in table 54. As usual, the maxima for the various measurements are found in the fossil specimens, indicating that the fossil gaur was a larger animal than the living one. The horn cores, however, are not particularly powerful in the Yenckingkou animals, although they are slightly longer than in the recent gaur. The comparison of the recent and fossil gaur skulls with those of the water buffalo shows that the gaur differs from the water buffalo in that the length from nasals to vertex is longer (220–285 mm. against 205–225 mm.), the length

from basion to lateral postpalatal notches is less (180–205 mm. against 200–220 mm.), the distance between orbit and base of horn core is longer (85–115 mm. against 55–75 mm.), and the occiput from basion to vertex is higher (245–310 mm. against 185 to ca. 225 mm.).

Because in the gaur the P_2 is reduced in size, this character enables us to identify several rami of the mandible in which this tooth is preserved.

The metapodials of the "elongated" type in the Yenckingkou collection show an excess in size over their recent homologues in *Bibos gaurus*, as was to be expected.

The fossil *Bibos* from Yenckingkou is distinguishable from recent *Bibos gaurus* only by its greater size. It seems advisable to give a new subspecific name to the remains now

TABLE 57

MEASUREMENTS (IN MILLIMETERS) OF THE METATARSALS IN RECENT AND FOSSIL *Bibos gaurus*

	Length	Proximal Width	Middle Width	Distal Width	Ratio: Distal Width/Length
<i>B. gaurus</i>					
A.M.N.H.(M.) Nos.					
112979	271	60	39	64	0.24
54470	259	63	38	67	0.26
<i>B. g. grangeri</i>					
A.M.N.H. Nos.					
39213	312	66	41	74a	0.24a
39213	312	68	46	77	0.25
39210	310	72	47	77	0.25
39210	310	59	38	63	0.20
39214	301	60	40	67	0.22

under discussion with a view to the fact that *Bibos geron* Matsumoto, as said above, is based on teeth that may be either *Bubalus bubalis* or *Bibos gaurus* and thus is taxonomically indeterminable.

We take pleasure in dedicating the Yenchingkou race of *Bibos gaurus* to the memory of Dr. Walter Granger, who was responsible for collecting the material on which *Bibos gaurus grangeri* is based.

CAPRICORNIS OGILBY

Capricornis OGILBY, 1837, Proc. Zool. Soc. London, for 1836, p. 139.

GENERIC TYPE: *Antelope thar* Hodgson.

DIAGNOSIS: Horn cores closely set, rising just behind the orbits, more or less nearly in the plane of the face, almost straight, tapering, rounded in cross section, and diverging outward. No postorbital pit. Occipital surface forming an obtuse angle with parietal plane, facial portion moderately bent downward, nasal branch of praemaxillae usually not reaching nasals, large but shallow lacrimal depression. Molars hypsodont, without accessory pillars.

Capricornis sumatraensis kanjereus,¹ new subspecies

TYPE: A.M.N.H. No. 18820, skull with both horn cores, front lacking.

PARATYPES: A.M.N.H. No. 18821, right mandibular ramus with P_3-M_3 ; 18823a, right mandibular ramus with P_3-M_3 .

REFERRED SPECIMENS: A.M.N.H. Nos. 18537, fragment of left maxilla with M_2^3 , also some associated phalanges; 18551, skull fragment with bases of horn cores; 18559, posterior portion of skull with right horn core complete; 18561, fragment of right maxilla with DM_4 , M_1^3 ; 18822a-c, three mandibular rami, (a) left P_4-M_1 , (b) right M_2-M_3 , (c) left M_1 ; 18823b, left mandibular ramus with M_2-M_3 ; 18824, right mandibular ramus with P_3-M_3 ; 18825a-b, maxillaries, (a) left P^2-M^2 , (b) right M_1^3 , also a cannon bone; 18826, two horn cores and some limb and foot bones; 18827, right mandibular ramus with DM_4 , M_1 .

HORIZON AND LOCALITY: Pleistocene; Yenchingkou, Szechwan, China.

DIAGNOSIS: Like modern *Capricornis sumatraensis* (Bechstein) but larger.

¹ "Kanjereus" (Dutch) means "large."

DISCUSSION

Capricornis remains have not before been recorded as fossils, but it is probable that the present finds are not the first evidence of fossil serows. The material in the collection from Yenchingkou is important because the specific identity with the living Sumatran serow can be made certain, and thus these finds establish the presence of the genus and species in the Pleistocene. The only difference worthy of notice is that of size; the fossil Chinese serow is larger, on the average, than any of the living forms (table 58).

We have tried to determine whether or not the Pleistocene Szechwan serow is closer to one of the Chinese races at present living than to the others, but the few characters that have been found to distinguish between the skulls of the various subspecies cannot be checked in the fossil material. Between *Capricornis sumatraensis milneedwardsii* and *C. s. argyrochaetes* (the latter considered as a distinct species by Lydekker, 1913, p. 196) skull differences are very minor (Jacobi, 1923, p. 20). *Capricornis s. montinus* Allen, perhaps confined to the high isolated snow peaks of the Likiang Range in the great bend of the Yangtze (Allen, 1940, p. 1234), differs from the other Chinese races in the shallower lateral notches of the posterior border of the palate. In *C. s. montinus* these postpalatal notches are stated to be behind the line of the posterior border of M^3 , while in *C. s. milneedwardsii* and *C. s. argyrochaetes* the notches extend forward beyond the posterior border of M^3 . However, as Anthony (1941, p. 120) remarks, two skulls from Burma differ so much in the depth of the postpalatal notches that the distinction is apparently a matter of variation with age.

There are three skulls of *Capricornis sumatraensis* from Burma in the American Museum of Natural History; in A.M.N.H. (M.) No. 119630, with M^3 erupting, the anterior border of M^3 is on the same line as the notches; in A.M.N.H. (M.) No. 115578, a young adult, the notches are on a line with the anterior half of M^3 ; while in the fully adult A.M.N.H. (M.) No. 114548 we find the notches on a line with the posterior part of M^3 .

The series of skulls of *Capricornis suma-*

TABLE 58
MEASUREMENTS (IN MILLIMETERS) OF THE SKULL AND TEETH OF RECENT
AND FOSSIL *Capricornis sumatraensis*

	Parietal Width	Width Over Horn Cores	Greater Diameter of Horn Core	Height of Occiput	M ¹⁻³	P ₃ -M ₃	M ₁₋₃
<i>C. s. argyrochaetes</i>							
A.M.N.H.(M.) Nos.							
45348	77	100	36	64	51	84	58
44778	77	92	31	68	54	—	—
44777	72	91	33	65	47	79	54
56982	70	82	27	59	51	—	—
56891	75	86	28	—	55	86	61
56979	72	80	28	64	52	83	59
56983	81	90	32	65	52	82	57
70451	76	84	30	—	54	84	59
84465	75	88	30	59	52	85	59
84464	75	87	28	63	50	81	56
84477	77	86	31	60	52	84	57
<i>C. s. milneedwardsii</i>							
A.M.N.H.(M.) Nos.							
110480	81	85	35	62	55	91	62
110478	76	90	34	69	—	—	—
<i>C. s. montinus</i>							
A.M.N.H.(M.) Nos.							
43037	80	97	36	65	50	81	56
43038	76	90	36	65	50	78	54
<i>C. s. kanjereus</i>							
A.M.N.H. Nos.							
18820, 18821	87a	87	33	63	—	97	68
18559, 18823a	78	84a	27	59	—	98	66
18551, 18561	—	88a	—	—	58	—	—
18826, 18825b, 18824	—	—	26	—	61	84	60

traensis argyrochaetes shows roughly the same condition. In two young adults [A.M.N.H. (M.) Nos. 44778 and 56982] the notches are on a line with the anterior half of M³, while in the series of adult skulls the lateral postpalatal notches vary in position from beside the middle to the posterior part of M³. There is only one fully adult skull in which the postpalatal notches extend as far forward as the middle of M³ [A.M.N.H. (M.) No. 56979].

The above observations tend to show that the last molar shifts forward relative to the palatal border with advancing age (a most common phenomenon), and that it is impossible in this respect to distinguish between the western and the eastern Chinese subspecies of *Capricornis sumatraensis*, *C. s. milneedwardsii*, and *C. s. argyrochaetes*, respectively.

In *Capricornis sumatraensis montinus*, however, we found, in contradistinction to Allen's remarks, that M³ is either slightly behind the lateral postpalatal notches (A.M.N.H. No. 43038), or the posterior border of M³ is just on a line with these postpalatal notches (A.M.N.H. No. 43037). Both of these skulls belong to fully adult, though not very old, individuals. Since even in old specimens of the other Chinese races (e.g., A.M.N.H. No. 44777, *C. s. argyrochaetes*) the postpalatal notches are more forward relative to M³, we may have here a difference that is valid, although "average" only.

As far as other evidence of fossil *Capricornis* goes, we find some references in the monograph by Pilgrim (1939, pp. 57-59) on the fossil Bovidae of the Siwaliks, but there the reference to the genus *Capricornis* is

TABLE 59
MEASUREMENTS (IN MILLIMETERS) OF MOLAR SERIES OF RECENT
AND FOSSIL *Naemorhedus goral*

	M ¹⁻³	M ₁₋₃
<i>N. g. griseus</i>		
A.M.N.H.(M.) Nos.		
110489	44	47
110483	43	47
110485	42	46.5
43030	40	45
43028	39	42
43004	39	41
<i>N. g. caudatus</i>		
A.M.N.H.(M.) Nos.		
45330	43	44
45488	42	45a
57292	42	46
<i>N. goral</i> , Yenchingkou		
A.M.N.H. No. 21787	43a	50a

vague and applied in the widest sense only. In the literature on the fossil mammals of China we find several references to goat antelope-like specimens, and we must say that *Pachygazella grangeri* Teilhard de Chardin and Young (1931, p. 40) of the Pontian of Shensi also recalls the recent serow. It is pointed out by the describers that this form cannot be referred to the genus *Naemorhedus* because of the compact structure and the sculpture of the horn cores and also because of the length of the skull.

The Yenchingkou fossils of *Capricornis* are well within the range of the living race *Capricornis sumatraensis milneedwardsii* and may belong to a race that was directly ancestral to the present subspecies of that region. However, there is at present no evidence that the fossil had closer relationships with that race than with any other subspecies of *Capricornis sumatraensis*, of which it is the first Pleistocene representative to be put on record.

NAEMORHEDUS SMITH

Naemorhedus C. H. SMITH, 1827, in Griffith, The animal kingdom . . . by . . . Cuvier, vol. 5, p. 352.

GENERIC TYPE: *Antilope goral* Hardwicke.

DIAGNOSIS: Like *Capricornis* but with basi-cranial axis much bent at the palate, no lacrimal fossa, and lacrimal separated from nasal.

Naemorhedus goral (Hardwicke)

Antilope goral HARDWICKE, 1825, Trans. Linnean Soc. London, vol. 14, p. 518.

REFERRED SPECIMENS: A.M.N.H. No. 21787, crushed skull with the bases of the horn cores, right P³-M³ and left M¹ (broken)-M³, right mandibular ramus with M₁₋₃, and left mandibular ramus with P₃-M₃, associated.

DIAGNOSIS: Horns short and sloping back from crest of forehead; tips almost straight.

DISCUSSION

The present specimen, although unmistakably belonging to *Naemorhedus goral*, is in a very bad state of preservation, which does not allow further identification. The muzzle and postorbital portion are very incomplete, and the mandible, too, is very defective. The molar series, however, is almost completely preserved.

There is little if any geographic differentiation in the recent subspecies in China today, although *Naemorhedus goral griseus* of western China, within the range of which the present fossil skull was found, is said to have shorter tooth rows than either *Naemorhedus goral caudatus* of northeastern China or *N. goral arnouxiianus* from the south (Allen, 1940, p. 1257). The measurements in table 59 tend to show that the molar series,

especially the lower series, are probably slightly longer in the fossil than in the recent forms. However, there is very much age variation in this kind of measurement, with the result that old skulls have shorter tooth rows than young adult ones, and the fossil specimen belongs to the latter group. If there is a difference in tooth size between the fossil and the recent forms it must be an "average" difference only, and the available single fossil specimen is not conclusive. Although the teeth of the fossil goral of

Szechwan seem to differ from their recent homologues in the same point in which those of most of the Yenchingkou mammals differ from the corresponding recent mammals, we feel that in the present case there is no justification for the erection of a new subspecific name. It can be added that there seems to be no reliable difference between the north-eastern and the western recent race of *Nae-morhedus goral* so far as the length of the tooth series is concerned.

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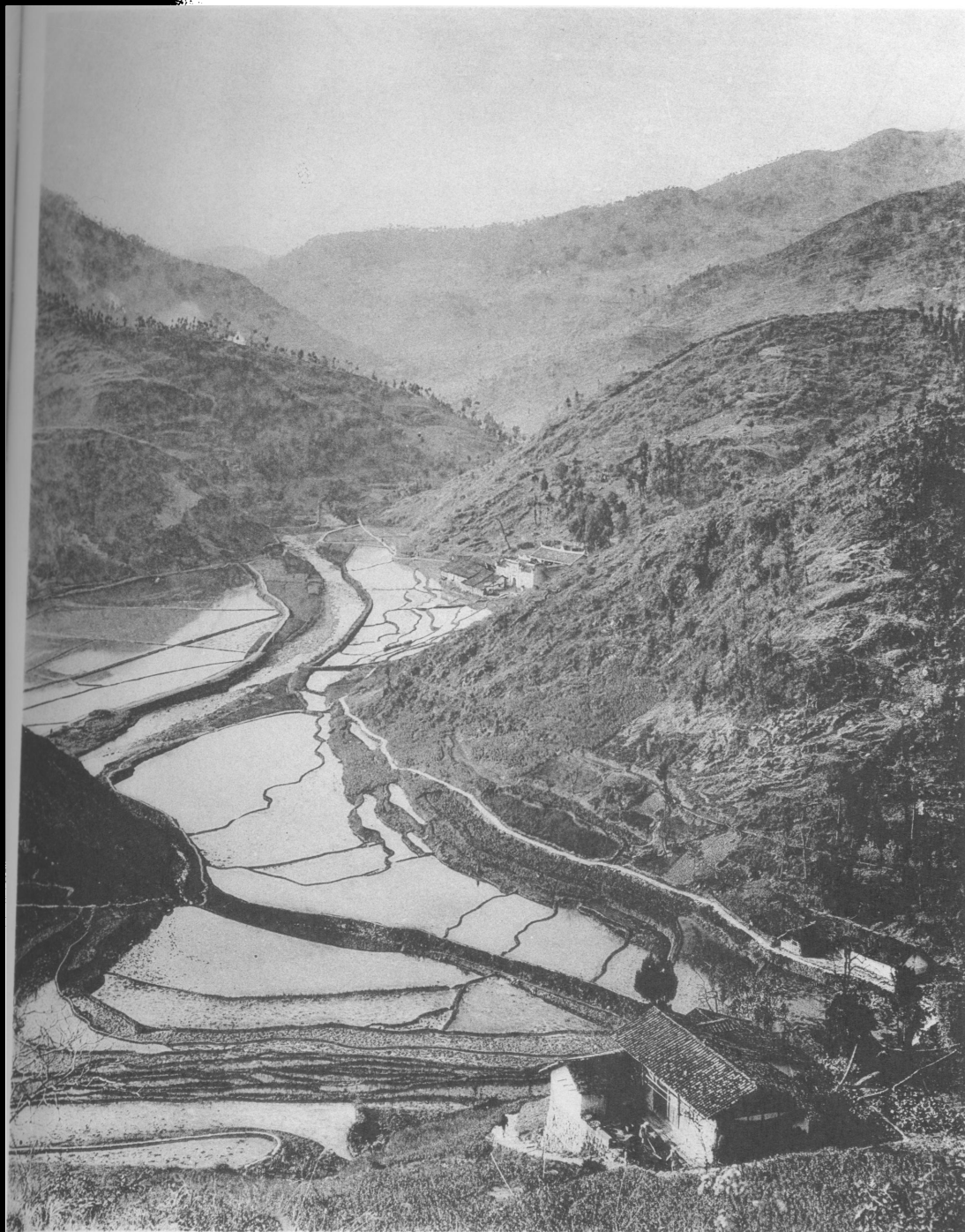
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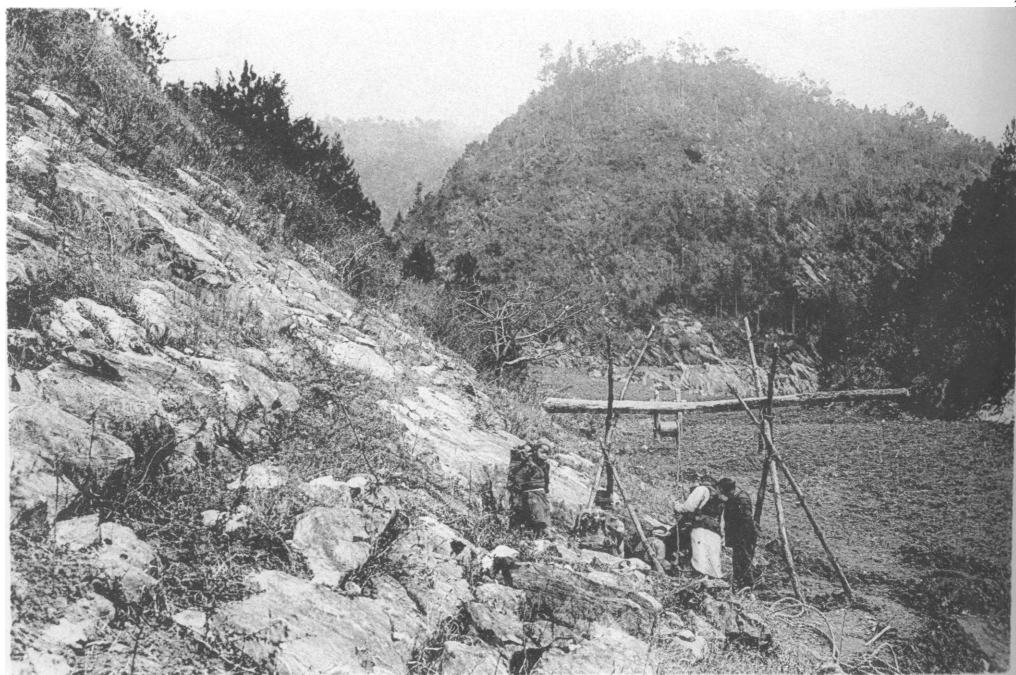
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Yenchingkou; looking down the valley towards the Yangtze, from near the base of the Dragon Bone ridge

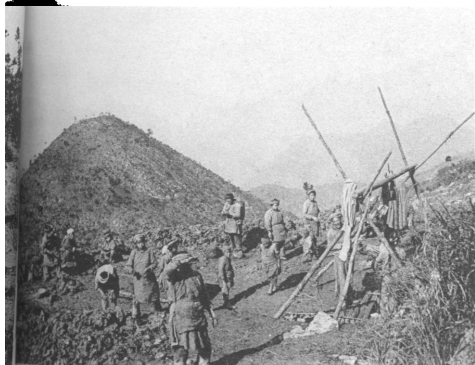


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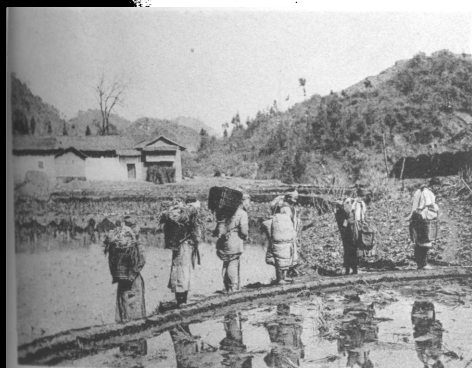
1. The upper village of Yenchingkou with the temple in which the party lived during three weeks
2. A highly fossiliferous pit in working order on the Dragon Bone ridge



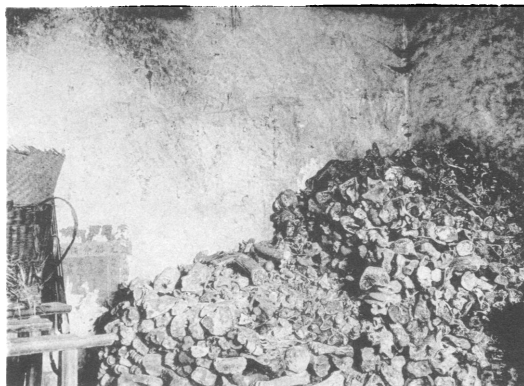
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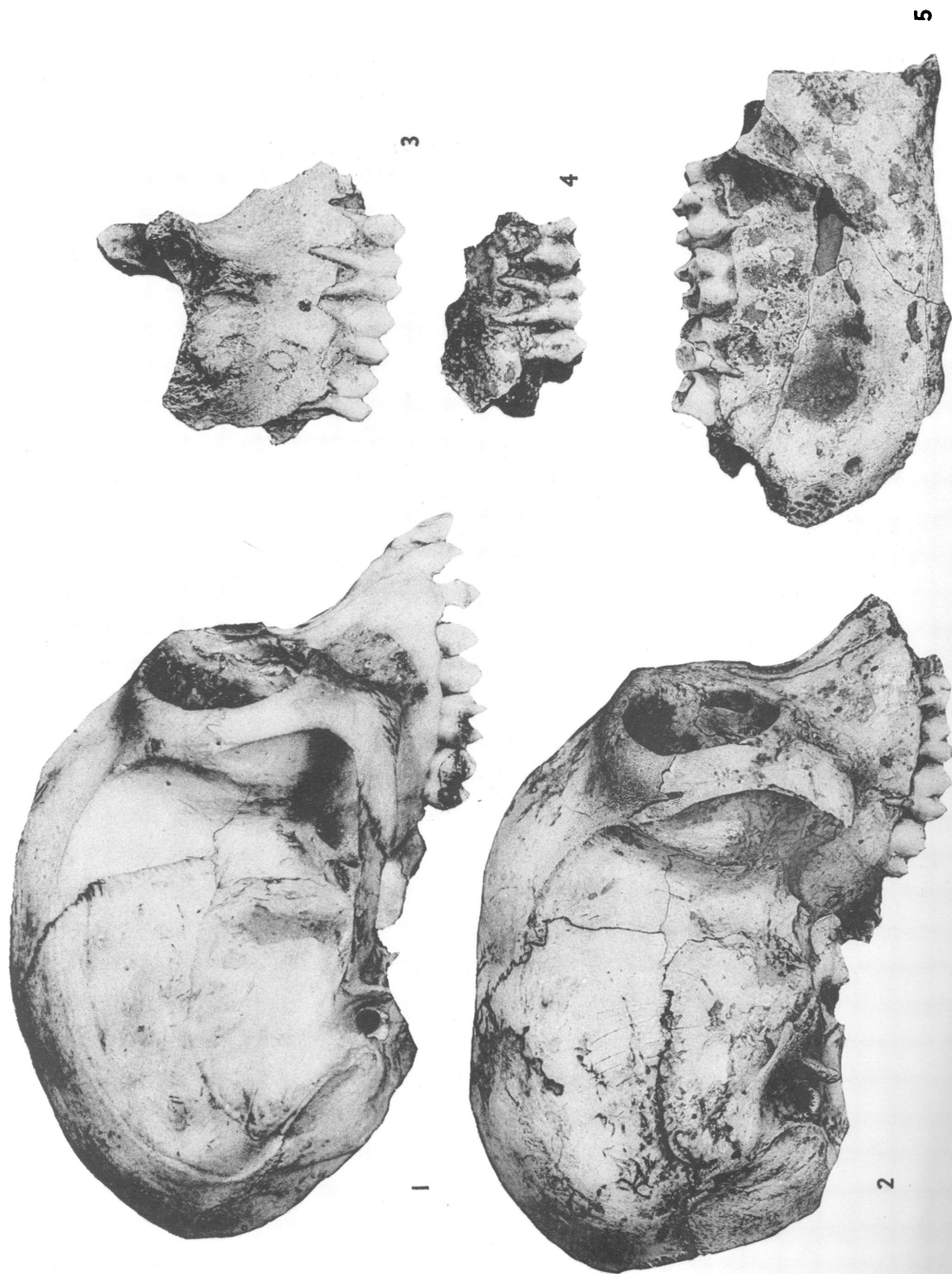


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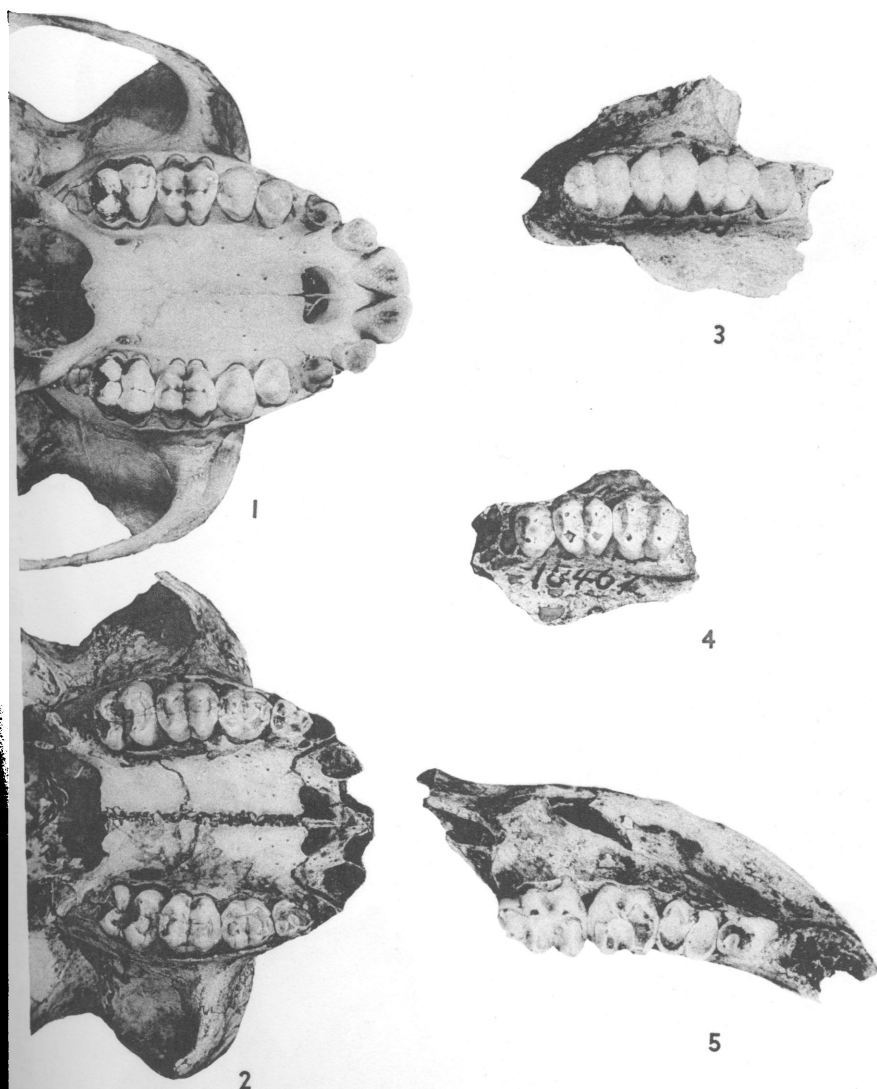


5

5. The Dragon Bone ridge
excavated to a depth of 50 feet and yielded many fine specimens of *Rhinoceros*,
from the Dragon Bone ridge. The three near coolies bear baskets of
the property of a wholesale drug merchant
at Yenchingkou. Granger and Wong (front row) with assistants



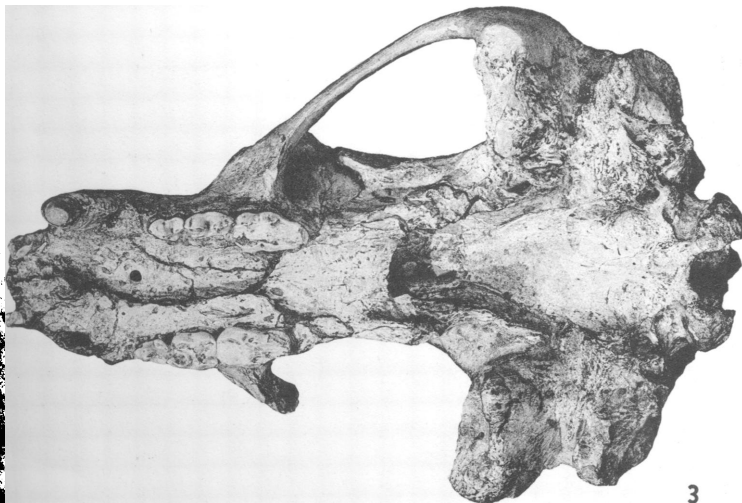
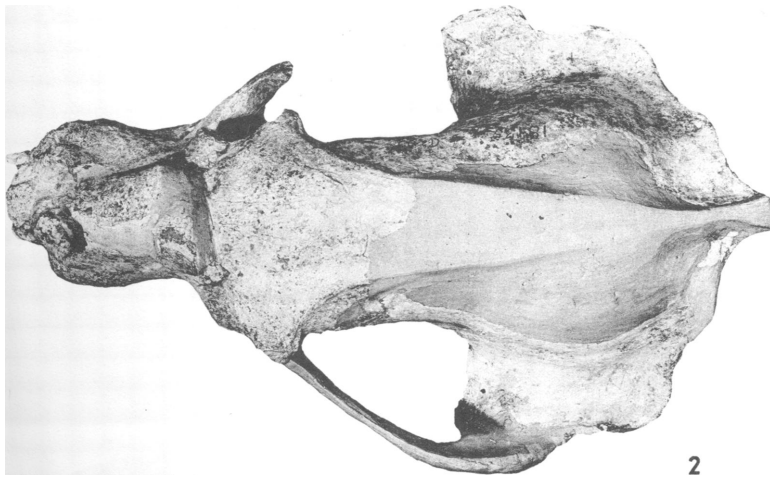
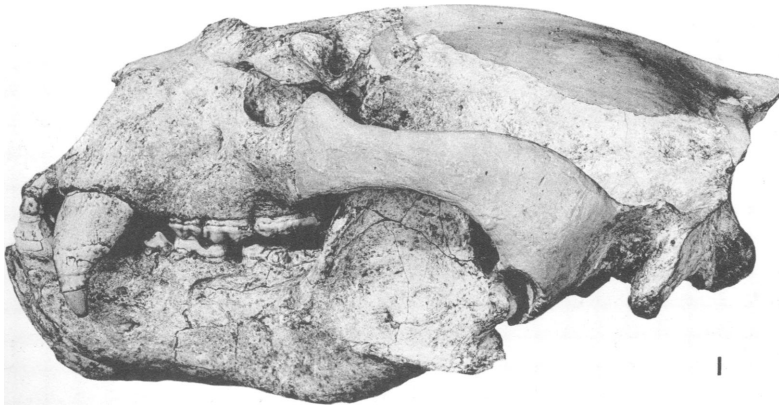
1. *Rhinopithecus roxellanae* Milne-Edwards. A.M.N.H.(M.) No. 110456, right lateral view.
2. Type, *Rhinopithecus roxellanae* Milne-Edwards. A.M.N.H. No. 18466, skull of subadult.
3. A.M.N.H. No. 18468, right lateral view. 4. A.M.N.H. No. 18469, right maxilla with P₄-M₃.
5. A.M.N.H. No. 18469, left lateral view.



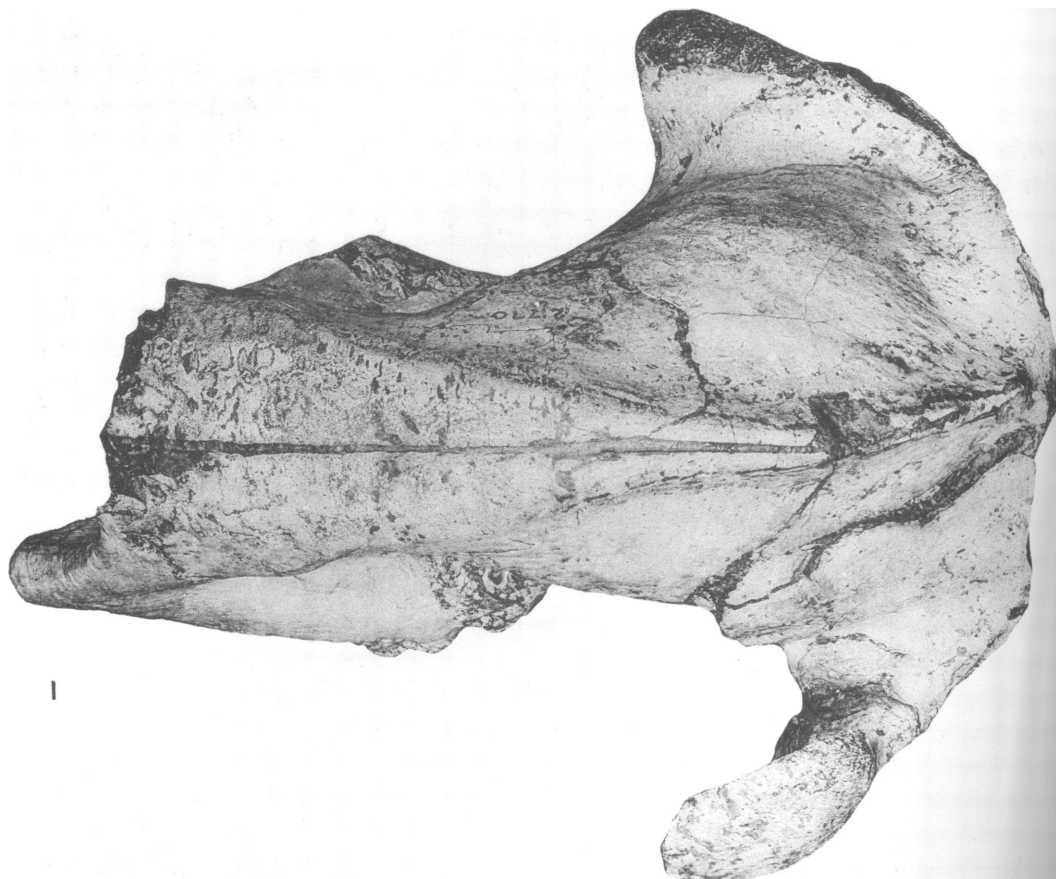
1. *Rhinopithecus roxellanae roxellanae* Milne-Edwards. A.M.N.H.(M.) No. 18456, skull, palatal view
 2-5. *Rhinopithecus roxellanae tingianus* Matthew and Granger. 2. Type, A.M.N.H. No. 18466, skull of subadult with milk molars and first two permanent molars, palatal view. 3. A.M.N.H. No. 18468, right maxilla with P_4-M_3 , crown view. 4. A.M.N.H. No. 18467, portion of left maxilla with P_4-M_3 , crown view. 5. A.M.N.H. No. 18469, left mandibular ramus with P_4-M_3 , crown view. All figures natural size



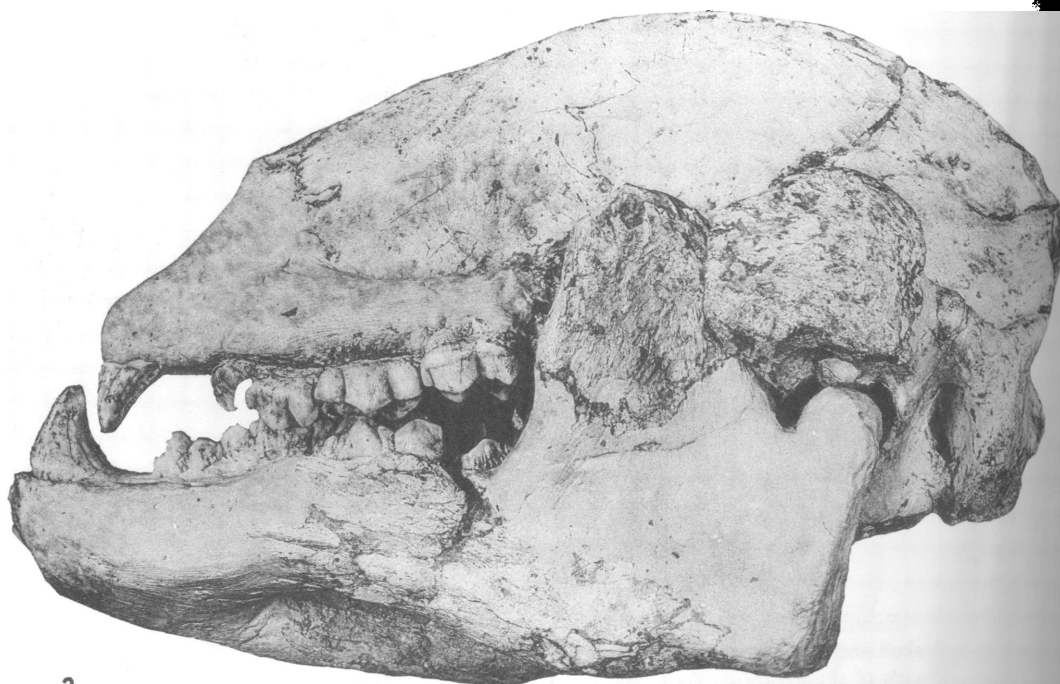
1-4. *Cuvon javanicus antiquus* Matthew and Granger. 1. A.M.N.H. No. 18727, skull with P-M₂. 2. Left lateral view. 3. A.M.N.H. No. 18389, fragment of left mandibular ramus with P-M₁. 4. Crown of tooth. 5. Skull and mandible, left lateral view. 6. Skull, palatal view. 7. Skull and mandible, left lateral view.



Euarctos kokeni Matthew and Granger. A.M.N.H. No. 18735, partial skull and lower jaw. 1. Left lateral view. 2. Dorsal view. 3. Palatal view of skull showing right and left P³-M¹. All figures one-third natural

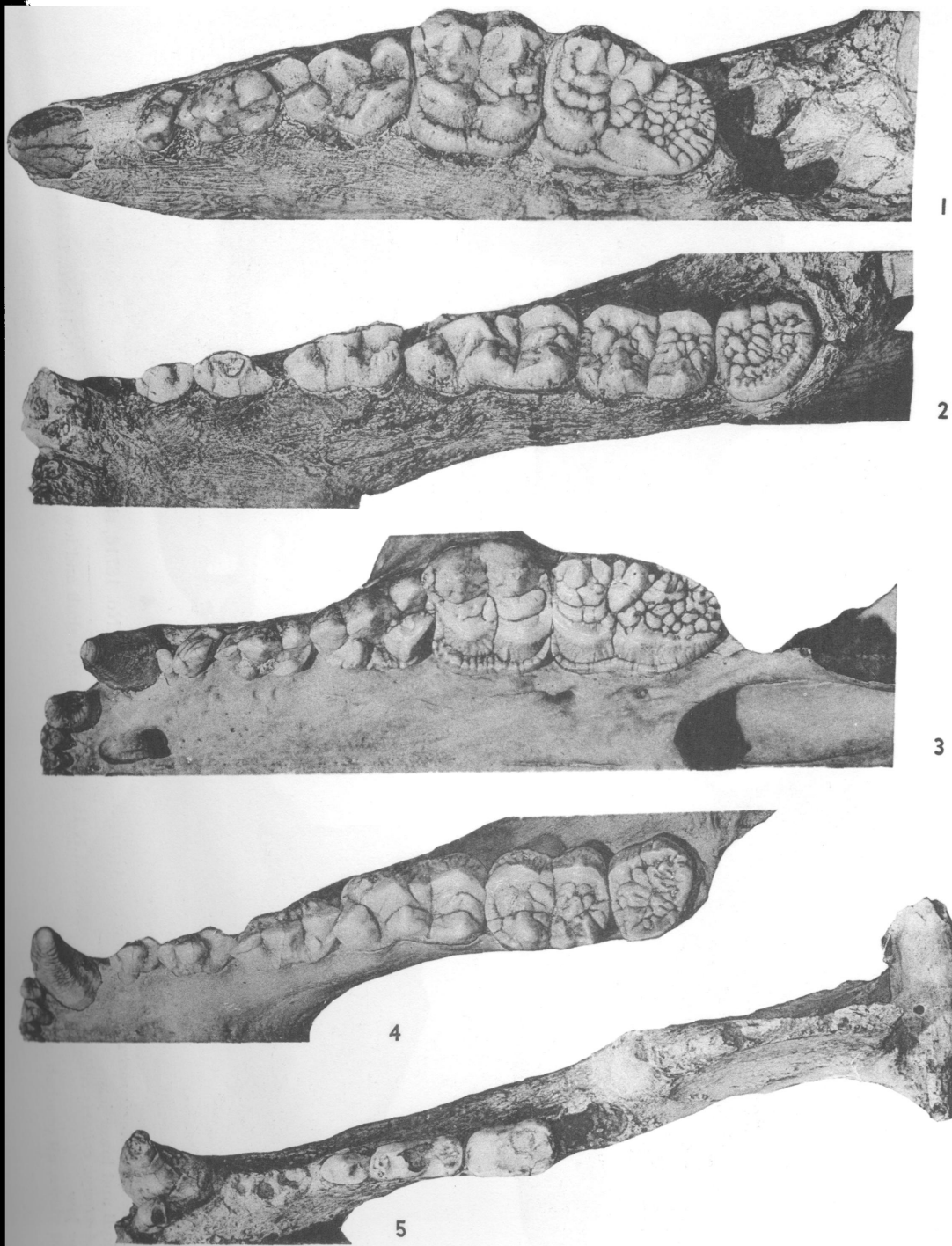


1



2

Ailuropoda melanoleuca fovealis Matthew and Granger. A.M.N.H. No. 21770, partial skull and lower jaw. 1. Dorsal view of skull. 2. Left lateral view. Both figures one-half natural size



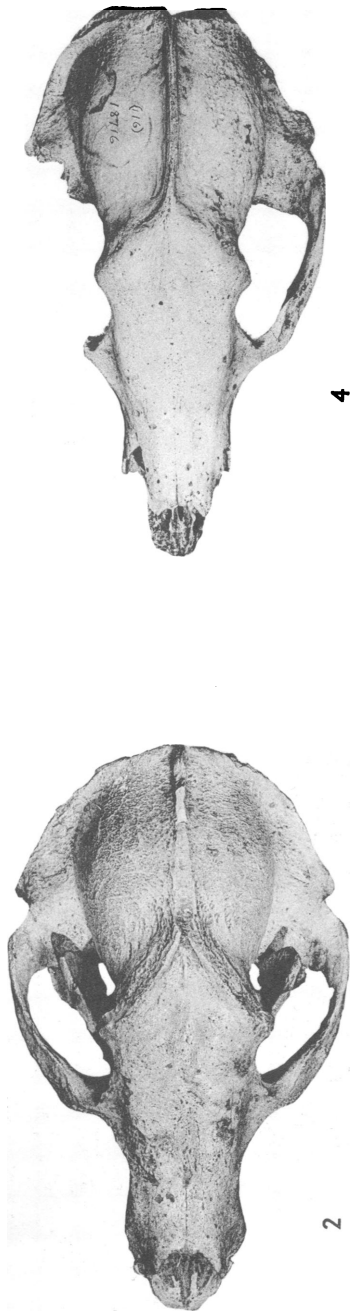
fovealis Matthew and Granger. A.M.N.H. No. 21770. 1. Left side of pal-
 andibular ramus with P_1-M_3

melanoleuca David. A.M.N.H.(M.) No. 110451. 3. Left side of palate.

and Granger. A.M.N.H. No. 18735, right mandibular ramus with P_1-M_2
 Three-quarters natural size; 5, two-thirds natural size



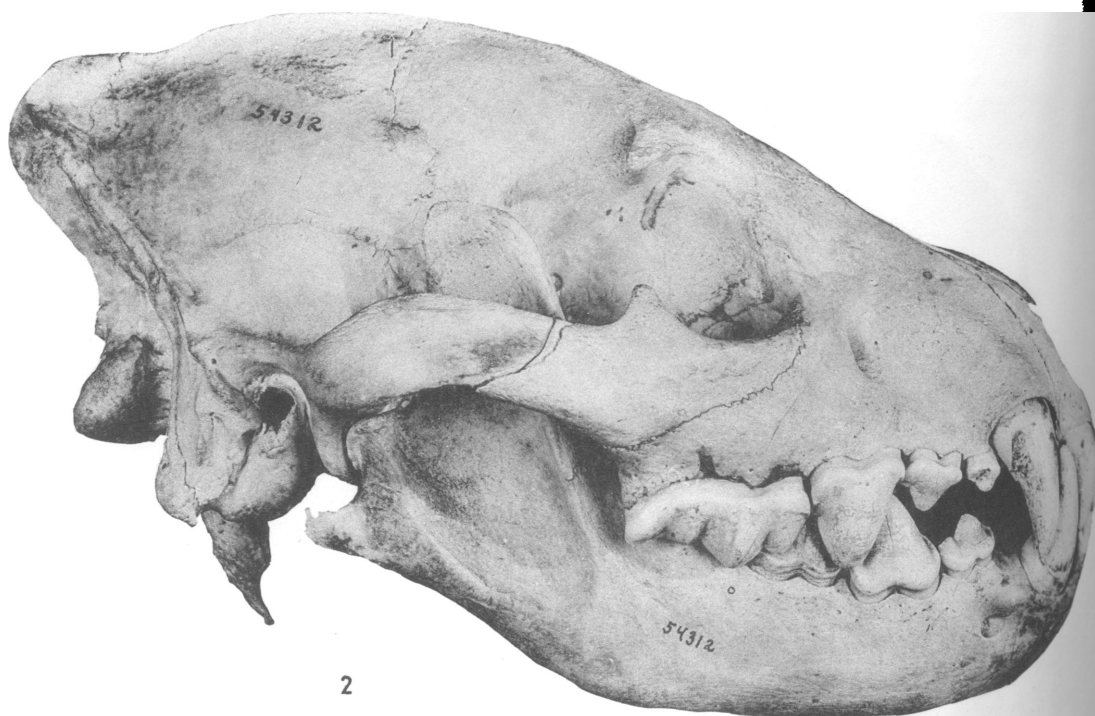
1, 2. *Arctonyx collaris rostratus* Matthew and Granger. 1. A.M.N.H. No. 18718, skull and lower jaw. 2. A.M.N.H. No. 21781, skull and lower jaw. 3. A.M.N.H. (M.) No. 84391, skull and lower jaw. 4. A.M.N.H. No. 18716, skull



1, 2. *Arctonyx collaris rostratus* Matthew and Granger. 1. A.M.N.H. No. 18718, skull. 2. A.M.N.H. No. 21781, skull
3, 4. *Arctonyx collaris collaris* Cuvier. 3. A.M.N.H.(M.) No. 84391, skull. 4. A.M.N.H. No. 18716, partial skull
Dorsal views, all one-half natural size



1



2

1. *Crocuta sinensis* Owen. A.M.N.H. No. 18730, partial skull and lower jaw, right lateral view.
 2. *Crocuta crocuta* (Erxleben). A.M.N.H.(M.) No. 54312, skull and lower jaw, right lateral view.
- Both figures three-quarters natural size



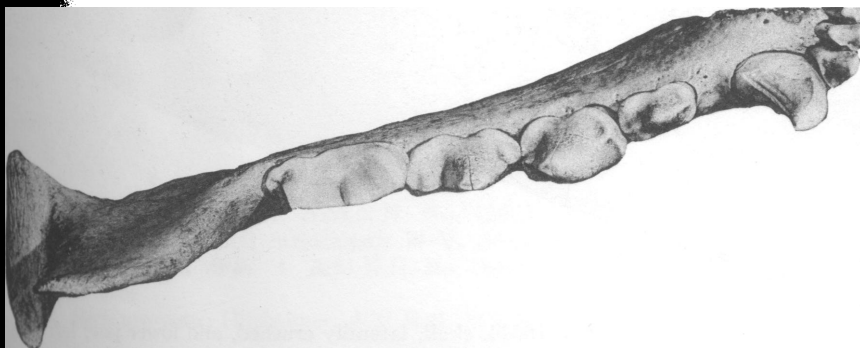
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2



3

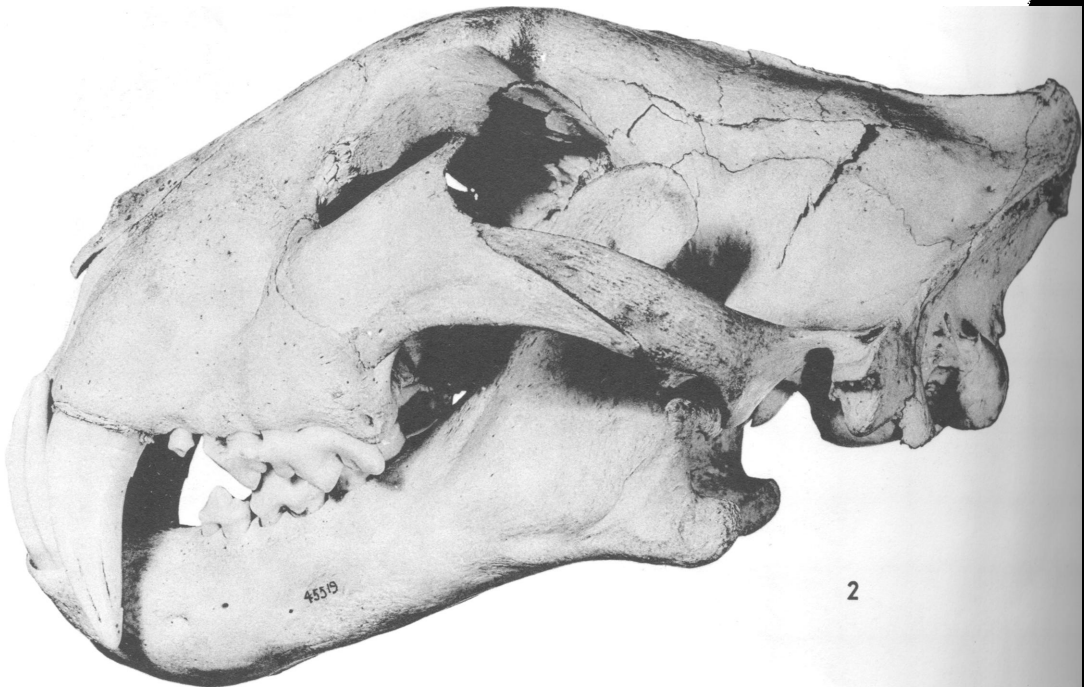


4

Acinaca sinensis Owen. A.M.N.H. No. 18730. 1. Right side of palate with C crown view. 2. Right mandibular ramus with C, P₂₋₄, and M₁, crown view. *Acinaca crocuta* (Erxleben). A.M.N.H.(M.) No. 54312. 3. Right side of palate with C, crown view. 4. Right mandibular ramus, crown view. All figures three-quarters natural size.



1

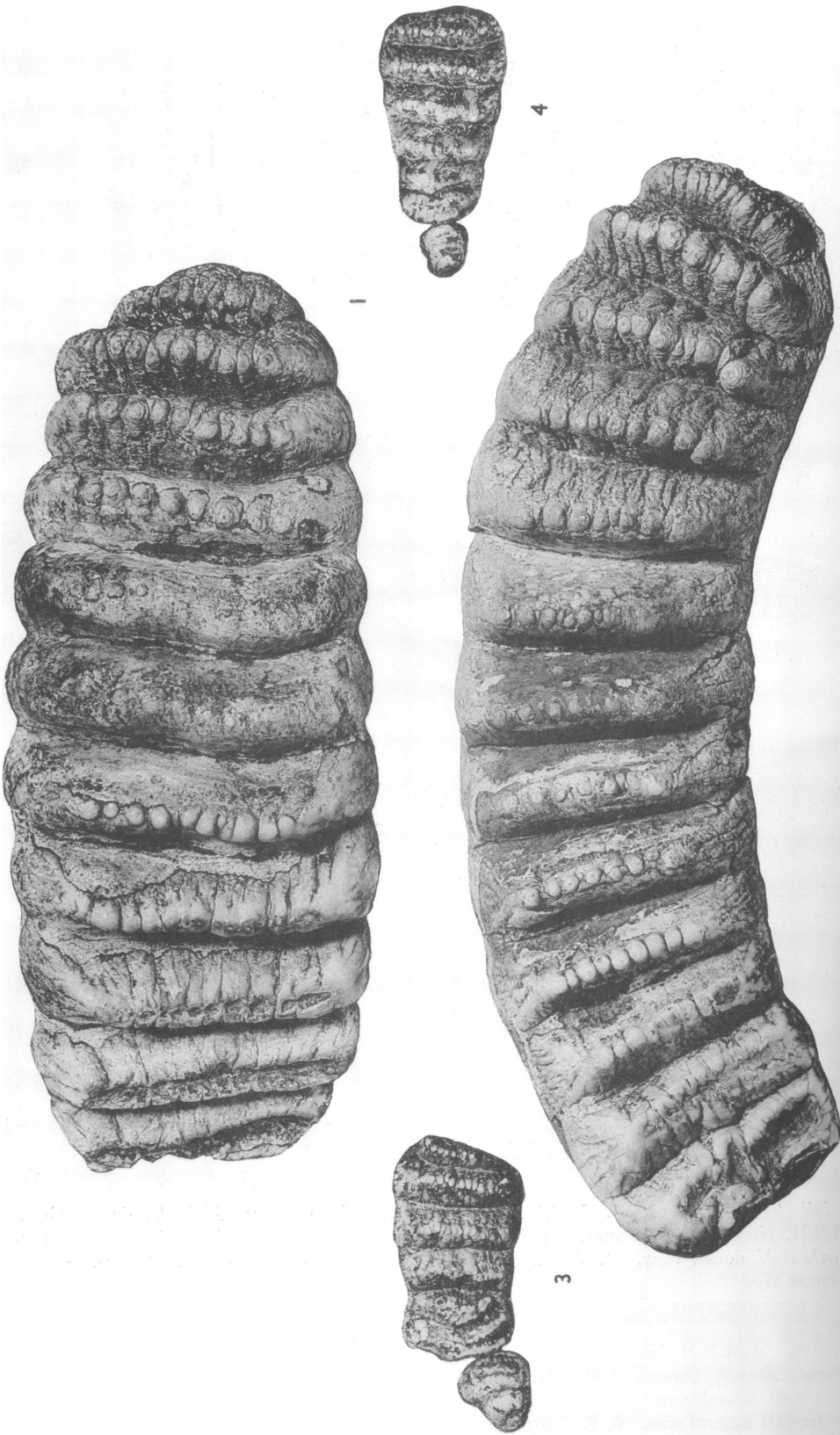


2

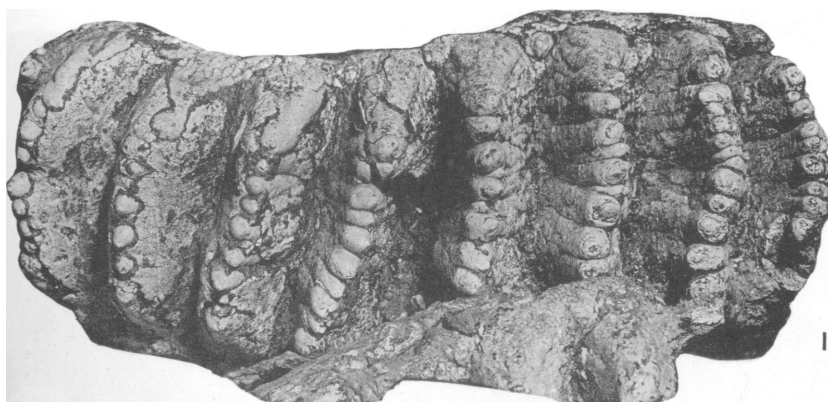
1. *Felis tigris* Linnaeus. A.M.N.H. No. 18624, skull, laterally crushed, and lower jaw, left
 2. *Felis tigris amoyensis* Hilzheimer. A.M.N.H.(M.) No. 45519, skull and lower jaw, left
- Both figures one-half natural size



is tigris Linnaeus. 1. A.M.N.H. No. 18688, right metacarpals II-V, dorsal view.
 H. No. 18672, left metacarpals II-V, dorsal view. 3. A.M.N.H. No. 18697, left
 II-V, dorsal view. 4. A.M.N.H. No. 18673, portion of right mandibular ramus with
 own view
tigris amoyensis Hilzheimer. A.M.N.H.(M.) No. 45519, right mandibular ramus, crown
 A.M.N.H. No. 21780, portion of right mandibular ramus with P_4-M_1 , lateral view
sinensis Owen. A.M.N.H. No. 18734, right mandibular ramus of juvenile with
 with, lateral view
 half natural size. 6, 7. Natural size.



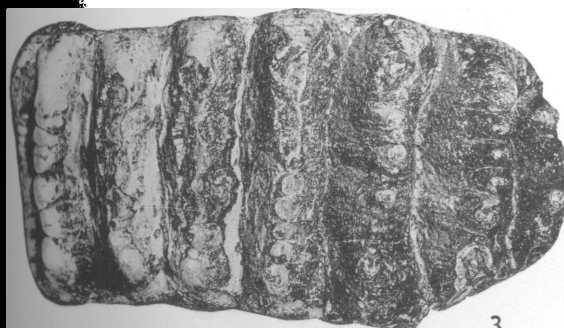
2
Left M^a. 3. 4. A.M.N.H. No. 18705. 3. Right DM^{a-3} (reversed). 4. Right



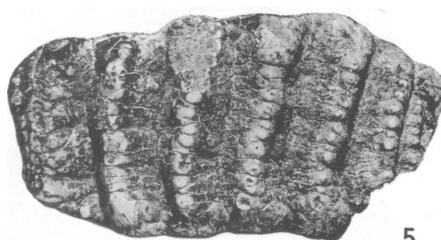
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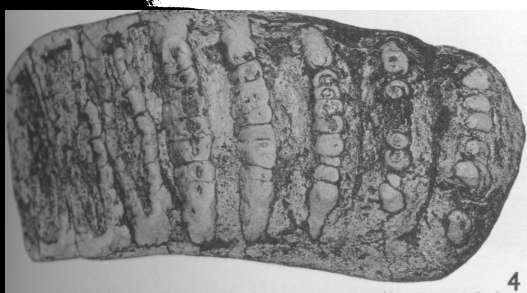
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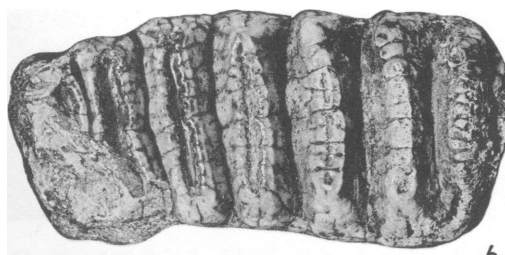
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5

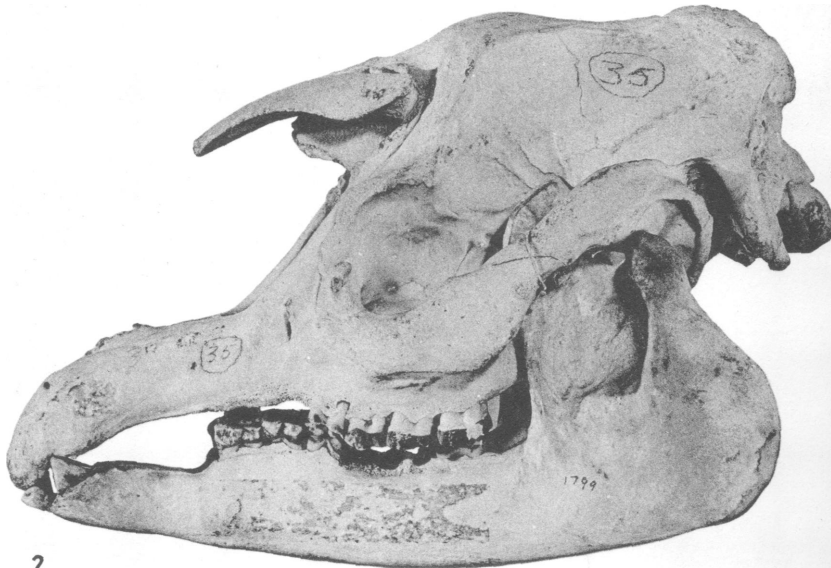


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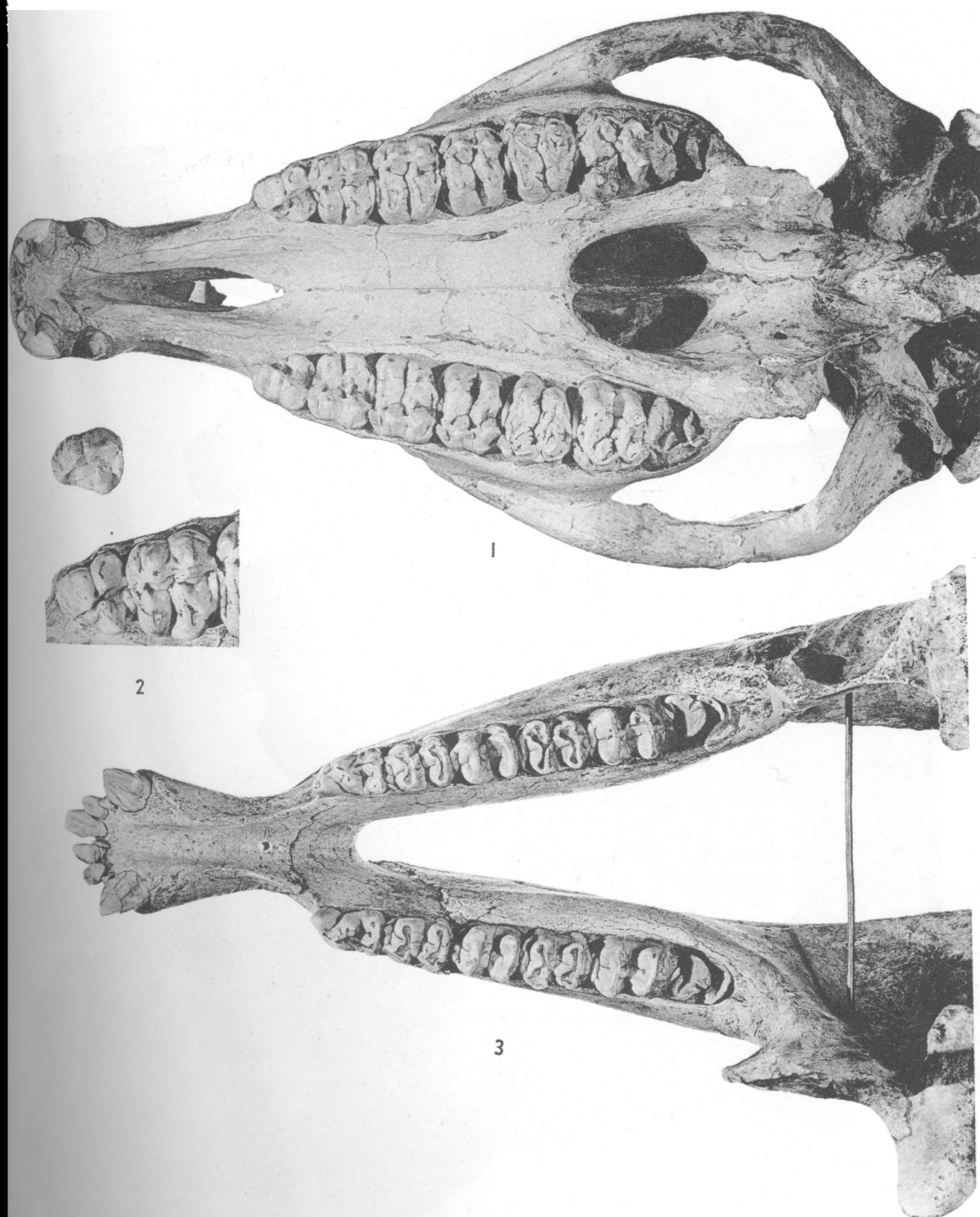
6

FIG. 1-4. A.M.N.H. No. 18636. 1. Left M_2 . 2. Right M_2 (reversed). 3. Left M_1 . 5. A.M.N.H. No. 18711, left DM_4 . 6. A.M.N.H. No. 18630a, left DM_4 . All figures half natural size

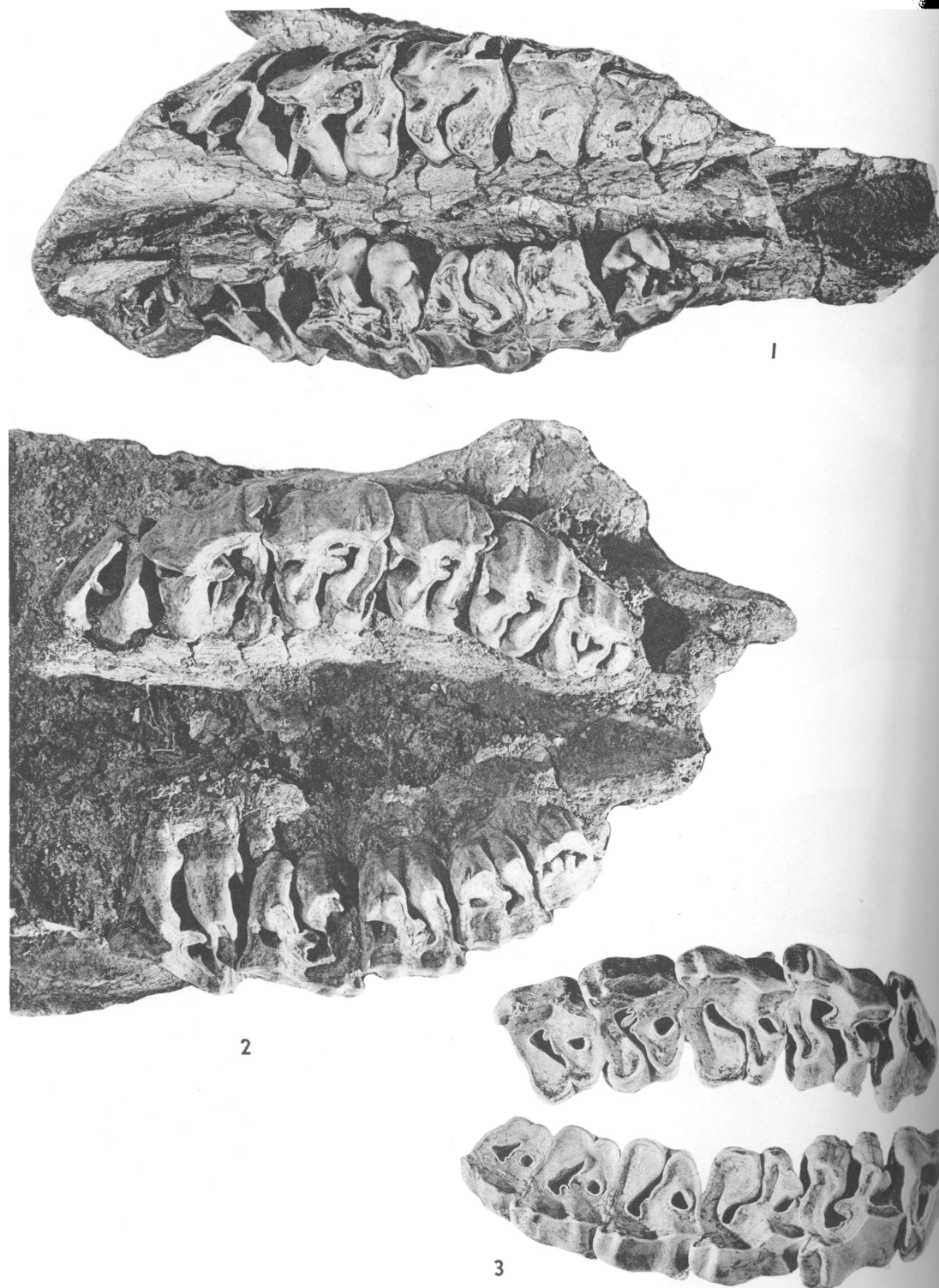


1. *Megatapirus augustus* Matthew and Granger. A.M.N.H. No. 18748, skull and lower jaw, lateral view

2. *Tapirus indicus* Desmarest. A.M.N.H. (M.) No. 1799, skull and lower jaw, left lateral view
Both figures one-quarter natural size



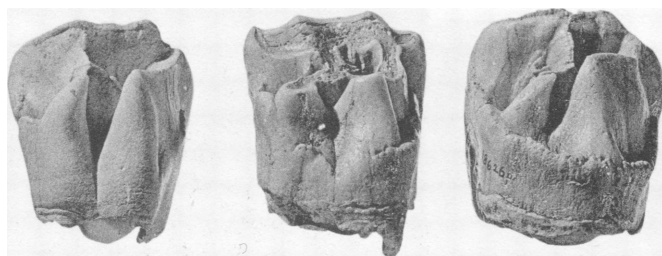
Augustus Matthew and Granger. A.M.N.H. No. 18748. 1. Skull, palatal view. One-third natural size. 2. Left P^{1-2} compared with A.M.N.H. No. 18460, left P^1 , to show variability in development of P^1 . One-half natural size. 3. Lower jaw, crown view. One-third natural size.



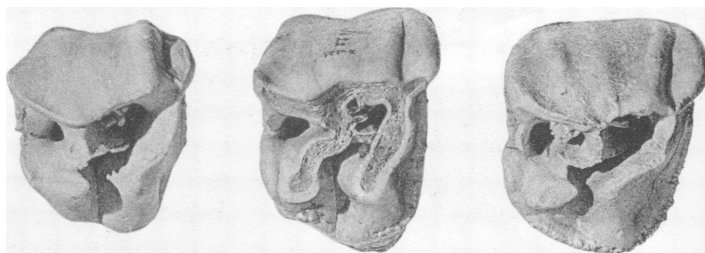
Rhinoceros sinensis Owen. 1. A.M.N.H. No. 18626, partial skull with right DM^1 , DM^1 , P^2 , DM^{3-4} , M^{1-2} (M^3 in alveolus), palatal view. 2. A.M.N.H. No. 18628, complete skull with right DM^1 , P^2-M^3 and left P^2-M^2 , palatal view. 3. C.N.H.M. No. P.14160, right P^2-M^3 associated, crown view. All figures one-third natural size



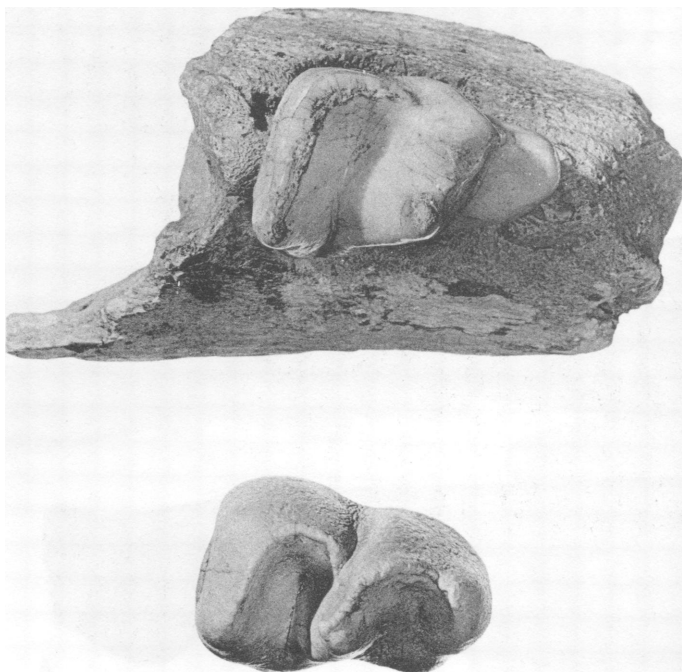
Owen. 1. A.M.N.H. No. 18606, maxilla with left P^3 - M^3 . 2. A.M.N.H. No. 18606, maxilla with left DM^1 - 4 and M^1 - 2 . 3. A.M.N.H. No. 18781, fragment of left mandibular ramus. 4. A.M.N.H. No. 18539, left DM_2 with posterior valley partly closed. 5. A.M.N.H. No. 18539, left mandibular ramus with DM_{2-3} , DM_4 broken. 6. A.M.N.H. No. 18758, left mandibular ramus with DM_2 , and anterior valley of DM_4 closed. All figures crown views. 1, natural size; 3-6, two-thirds natural size



1



2

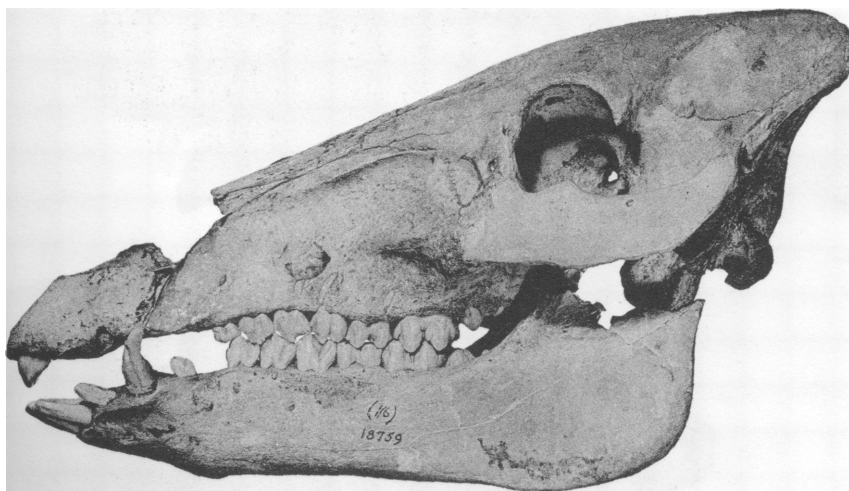


3

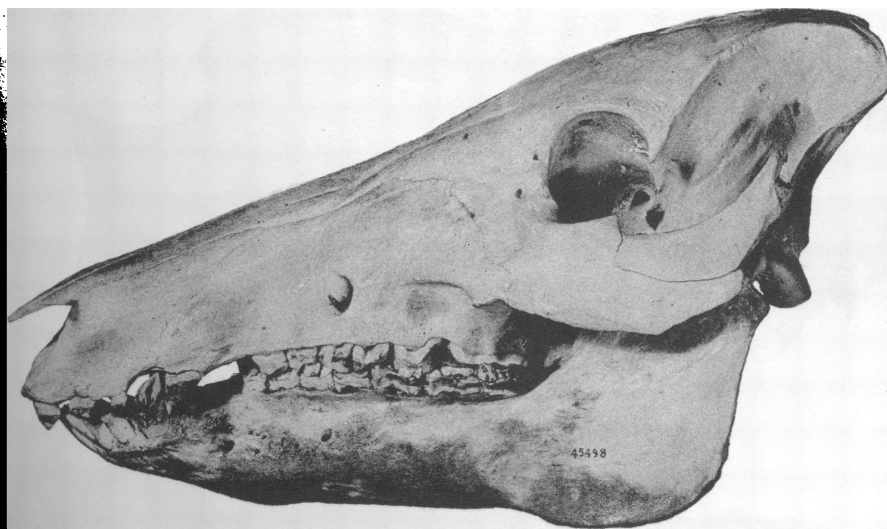


4

Rhinoceros sinensis Owen. 1, 2. A.M.N.H. Nos. 18780, 18622, and 18626a, three specimens of P^4 . 1. Lingual view. One-half natural size. 2. Crown view. One-half natural size. 3. Nos. 18780 and 18616, two specimens of left P_3 , showing constricted metacone in No. 18780 (top), normal development in No. 18616 (bottom), crown views. Natural size. 4. A.M.N.H. Nos. 18623 to be closed on the inside, while normal development is shown in No. 18787, right P_2 , showing posterior valley of both specimens. Natural size.



1

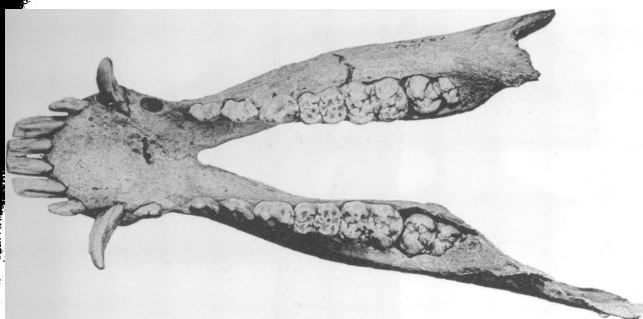


2

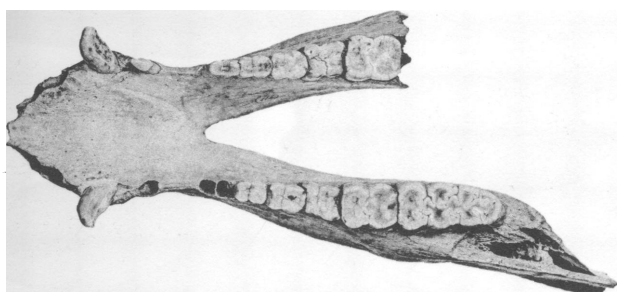
Microfa Linnaeus. 1. A.M.N.H. No. 18759, skull and lower jaw. 2. H.M. No. 45498, skull and lower jaw. Left lateral views, one-third size



Sus scrofa Linnaeus. 1, 2. A.M.N.H. No. 18759, skull. 1. Dorsal view. 2. Palatal view.
 3, 4. A.M.N.H.(M.) No. 45498, skull. 3. Dorsal view. 4. Palatal view. All
 one-third natural size



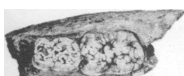
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2



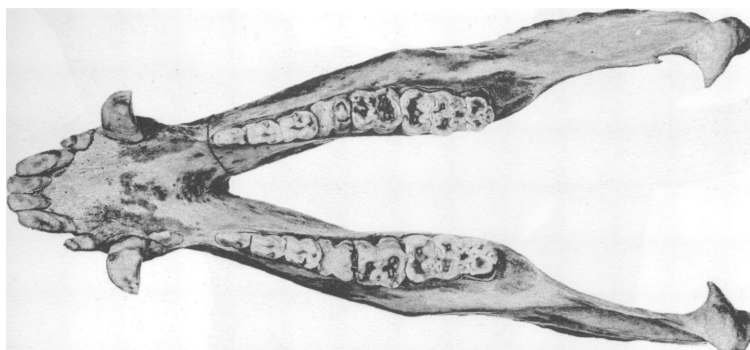
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4



6

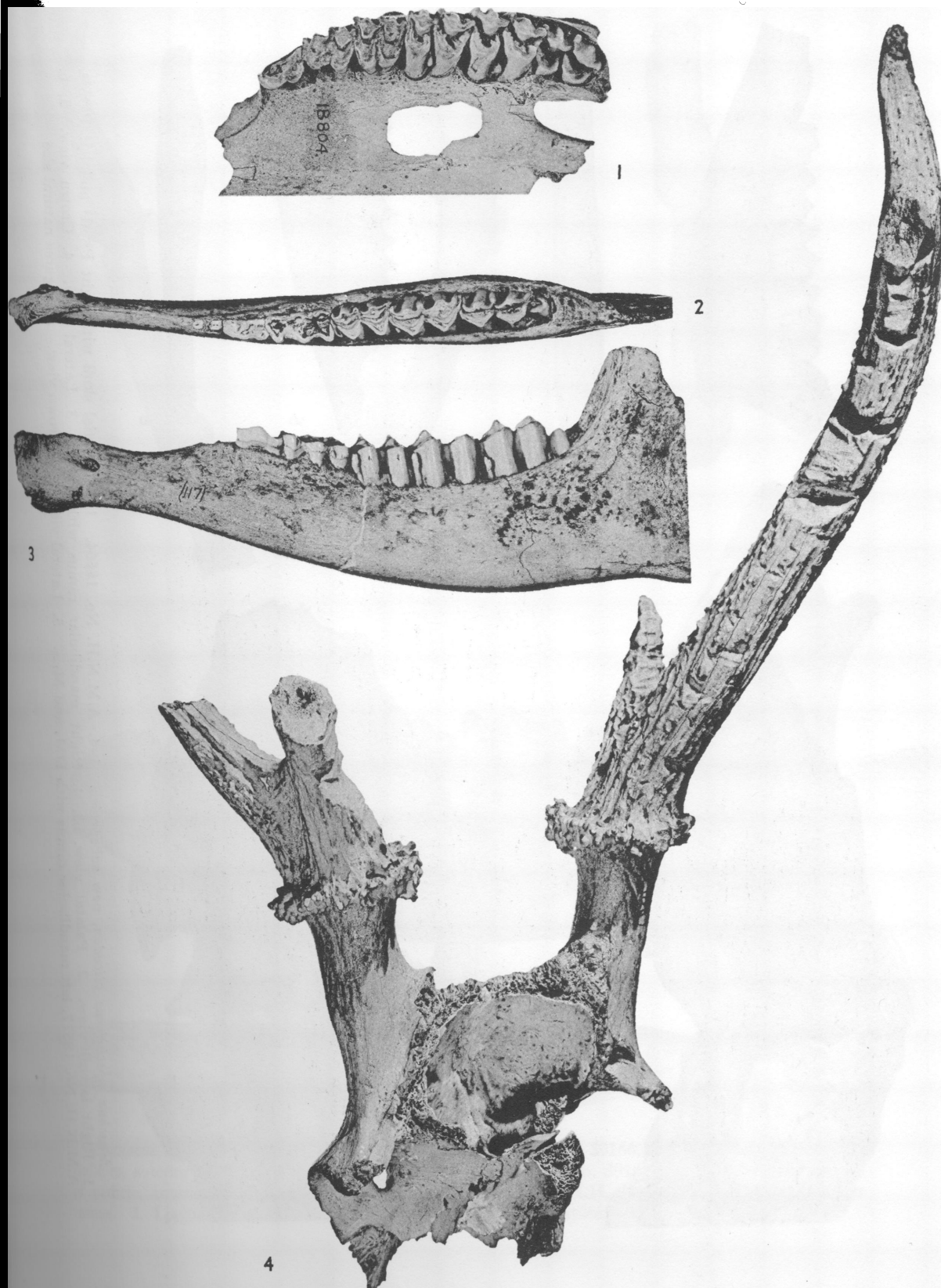


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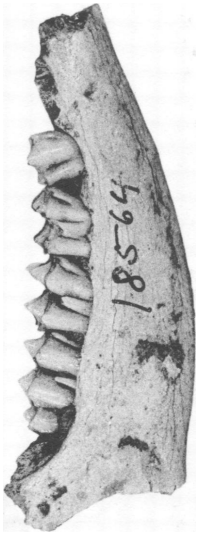
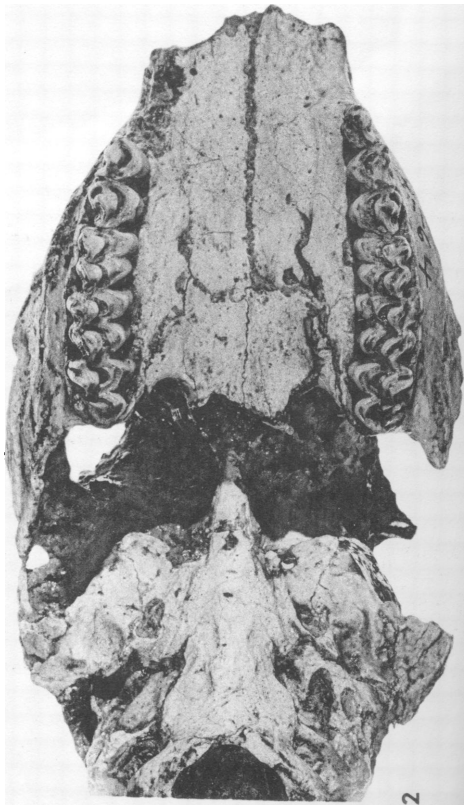
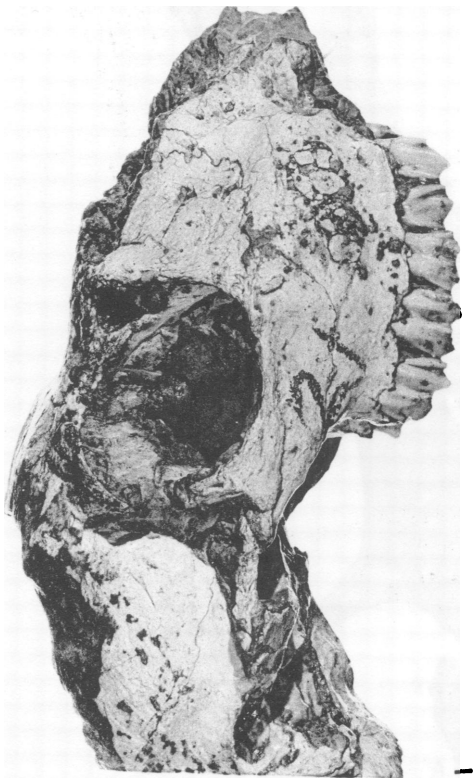
Sus scrofa Linnaeus. 1. A.M.N.H. No. 18759, partial lower jaw with right P_2-M_3 and left P_1-M_3 . 2. A.M.N.H. No. 18762, partial lower jaw with right P_1-M_2 and left P_3-M_3 , teeth well worn. 3. A.M.N.H. No. 18791, fragment of right mandibular ramus with P_4-M_3 . 4. A.M.N.H. No. 18447, fragment of right mandibular ramus with M_{1-2} . 5. A.M.N.H. (M.) No. 45498, lower jaw. 6. A.M.N.H. No. 18447, right P_4-M_2 . All figures crown views, one-third natural size



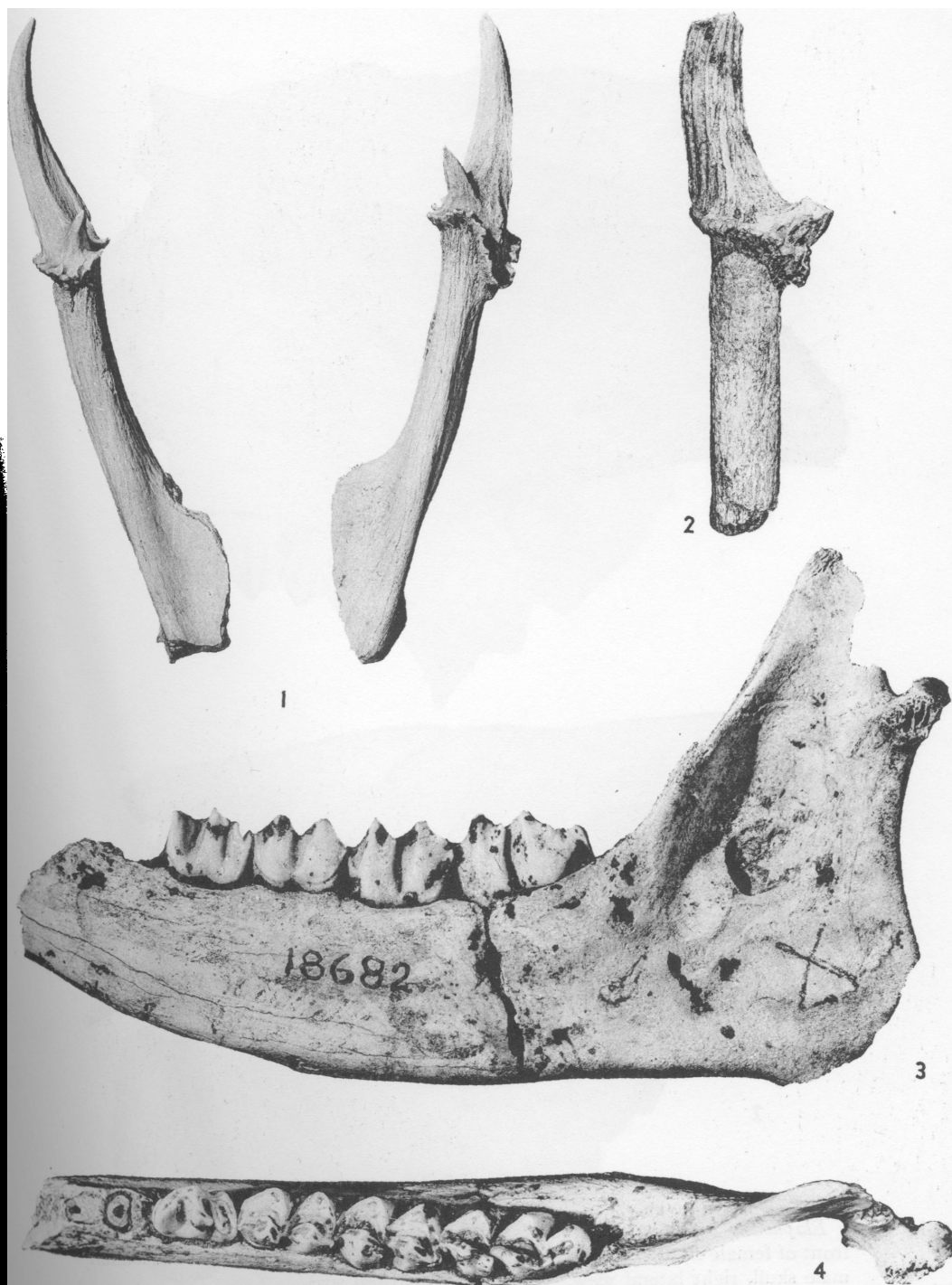
Rusa unicolor Kerr. A.M.N.H. No. 18814, partial skull with base of antlers.
1. Right lateral view. 2. Dorsal view. One-third natural size



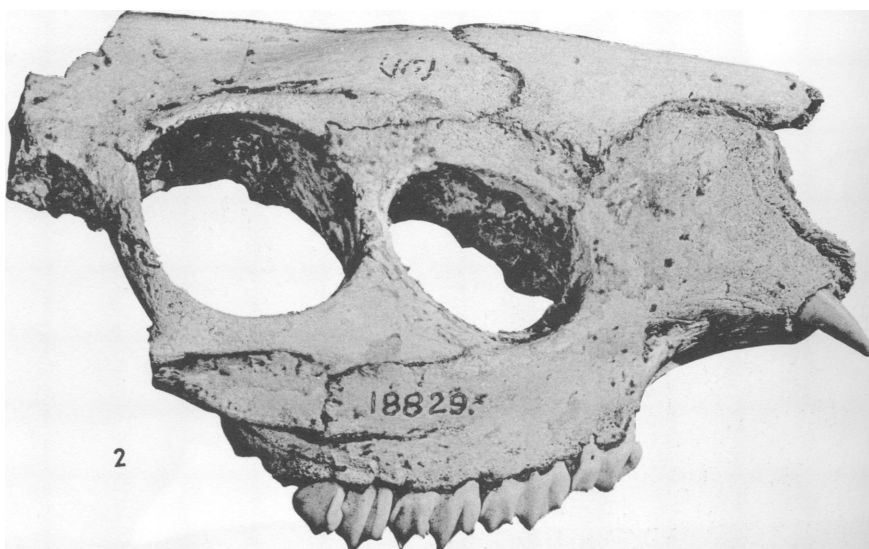
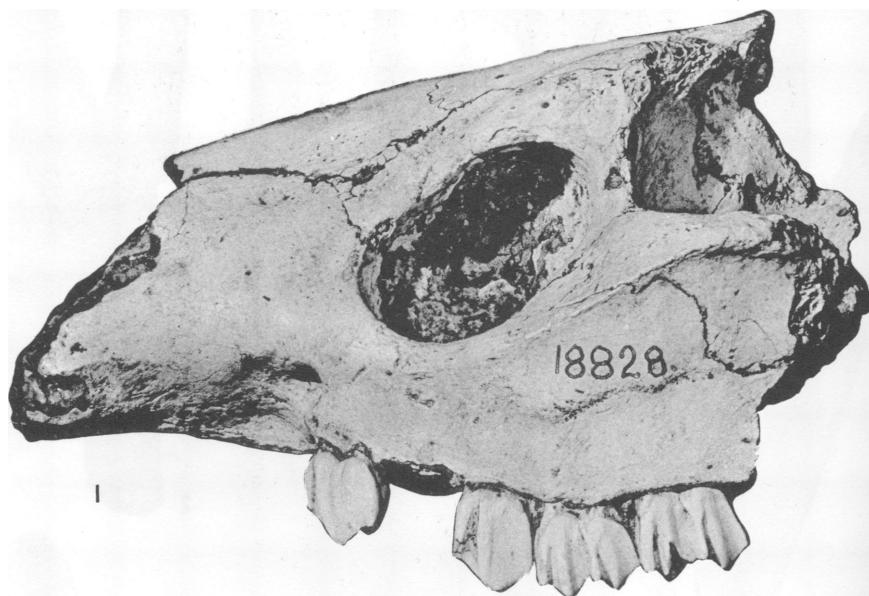
18804, left DM^{2-4} and M^{1-2} , crown view. 2, 3. A.M.N.H. No. 18805, M^{1-2} . 2. Crown view. 3. Lateral view. 4. A.M.N.H. No. 18806, showing rodent gnawings, posterior view.



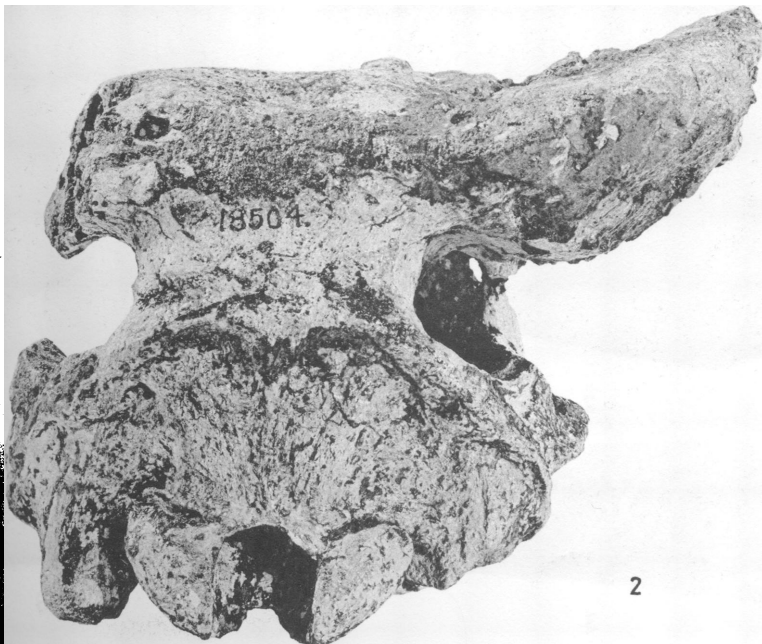
1-4. A.M.N.H. No. 18564. 1, 2. Partial skull with right P₁-M₃ and left P₁-M₃. 3, 4. Mandibular ramus with P₁-M₃. 5, 6. Crown view. All figures natural size.



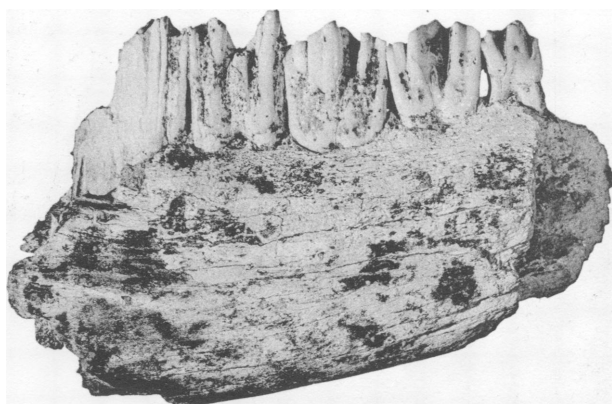
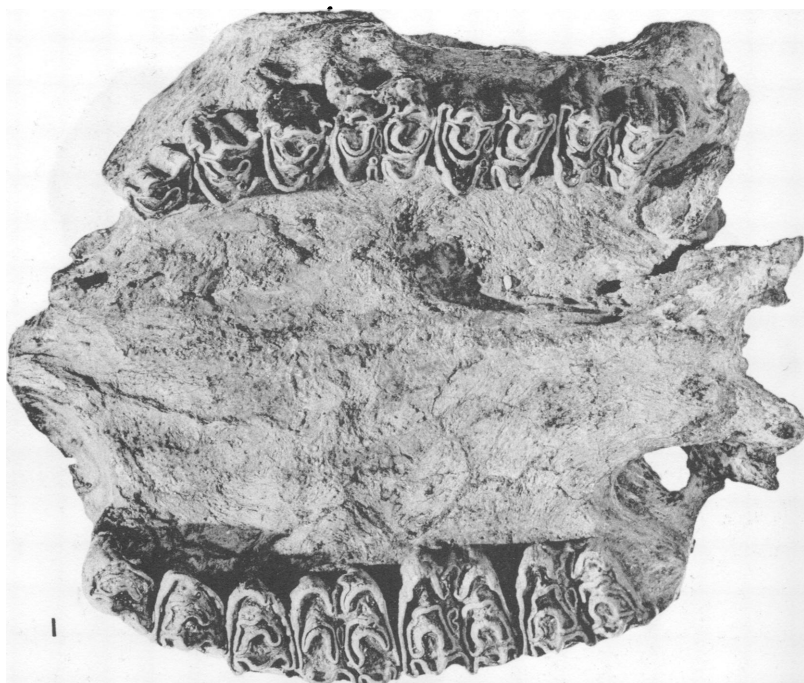
Rangifer marginatus Hooijer. 1. Type, A.M.N.H. No. 39166, right and left antlers and anterior view. One-half natural size. 2. A.M.N.H. No. 39165, right antler and portion anterior view. One-half natural size. 3, 4. A.M.N.H. No. 18682, right mandibular anterior view. Natural size. 4. Crown view. Natural size



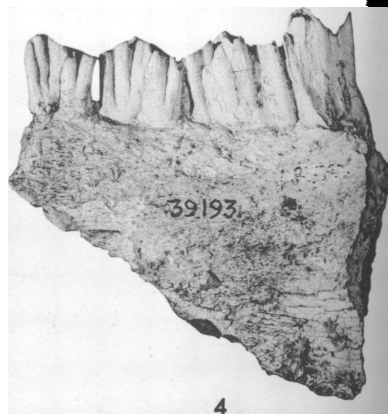
Elaphodus cephalophus megalodon Hooijer. 1. Type, A.M.N.H. No. 18828, front of female skull, left lateral view. 2. A.M.N.H. No. 18829, front of subadult male skull, right lateral view. Both figures natural size



Bubalus bubalis Linnaeus. A.M.N.H. No. 18504, partial skull with base of right horn core. 1. Dorsal view. 2. Occipital view. Both figures one-fourth natural size



2



4



3



5

Bubalus bubalis Linnaeus. C.N.H.M. No. P.14152, palate with right and left P_2-M_2 , crown view.
 2, 3. *Bibos gaurus grangeri*, new subspecies. A.M.N.H. No. 39192, left mandibular ramus with P_2-M_2 . 2. Lingual view. 3. Crown view.
 4, 5. *Bubalus bubalis* Linnaeus. A.M.N.H. No. 39193, right mandibular ramus with P_2-M_2 (broken). 4. Lingual view. 5. Crown view.
 All figures one-half natural size



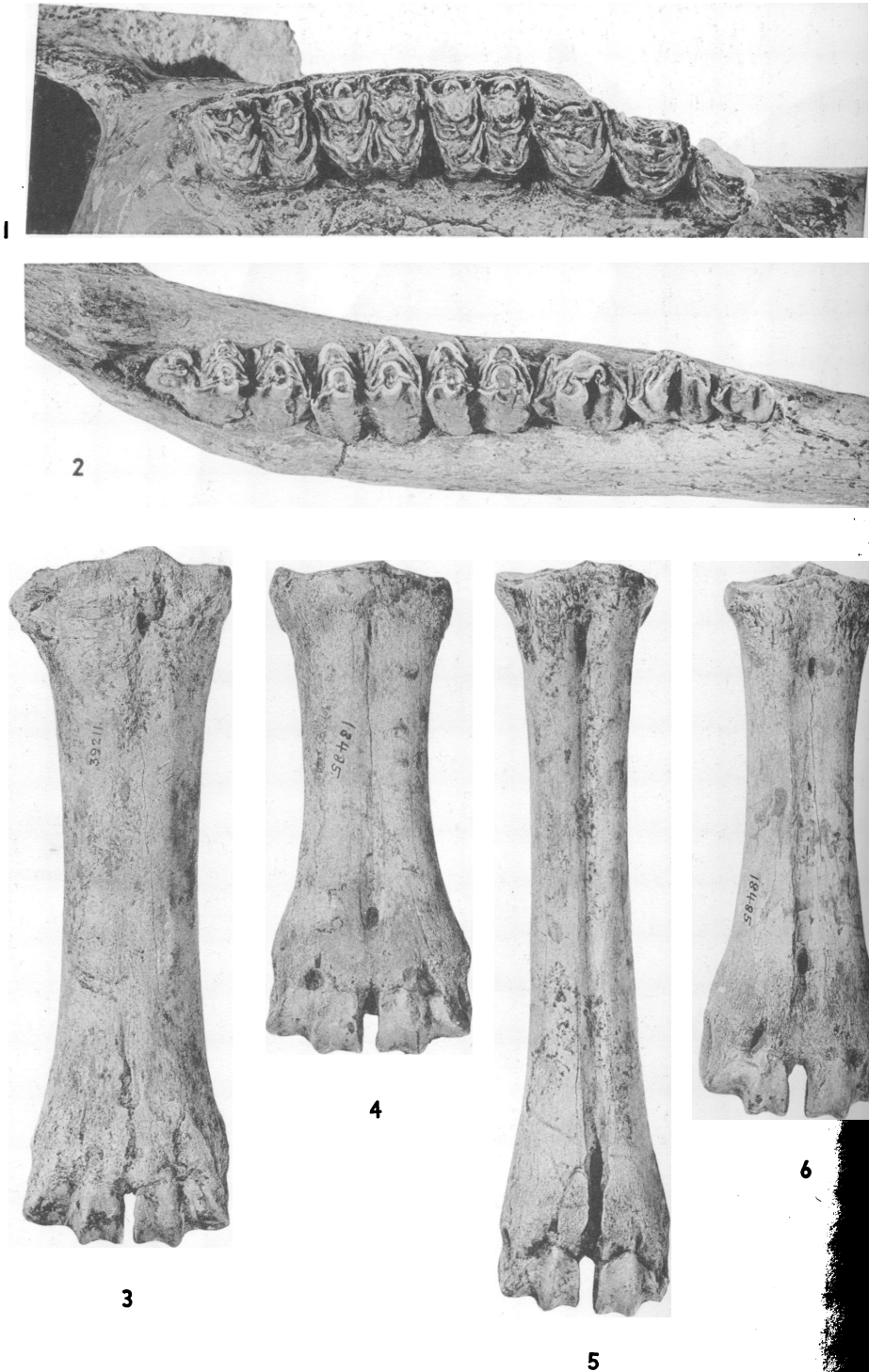
Bibos gaurus grangeri, new subspecies. 1. A.M.N.H. No. 39188, skull. 2. Type, A.M.N.H. No. 18465, skull. Both figures occipital view. 1. One-fourth natural size; 2, one-fifth natural size



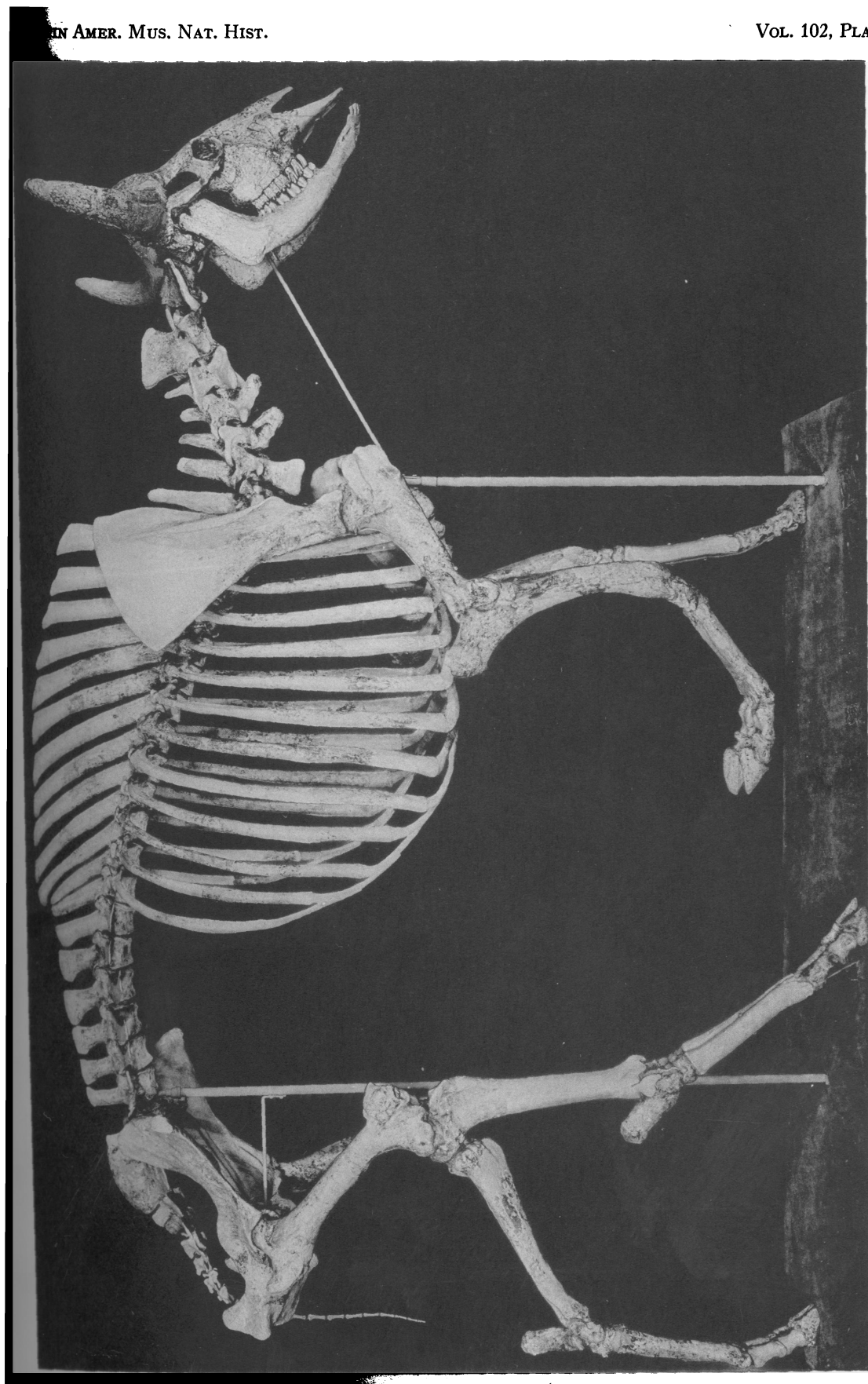
Stylonychia grossi, new subspecies. Type, A.M.N.H. No. 18465, skull and lower jaw, right lateral view. One-fourth natural size



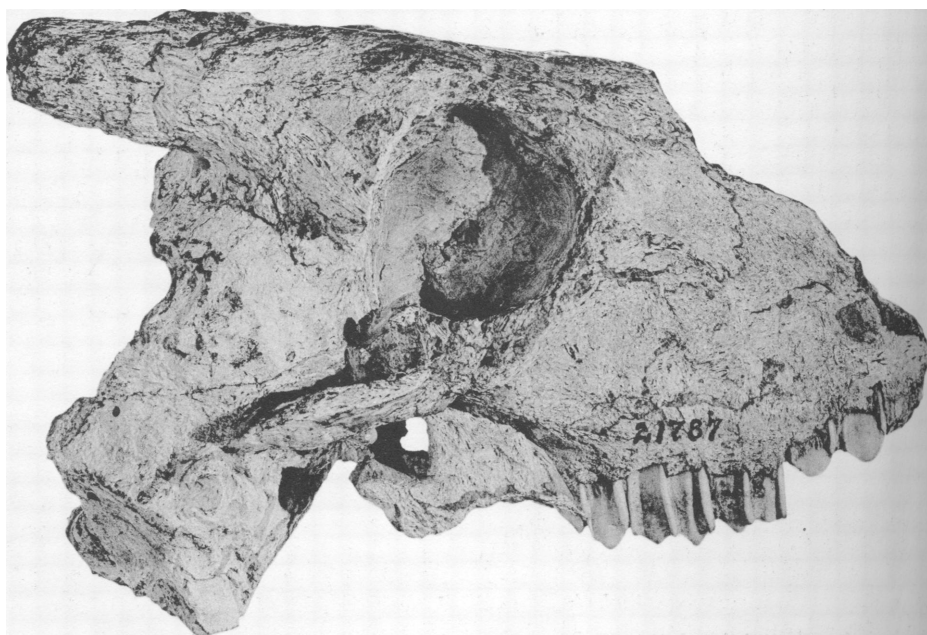
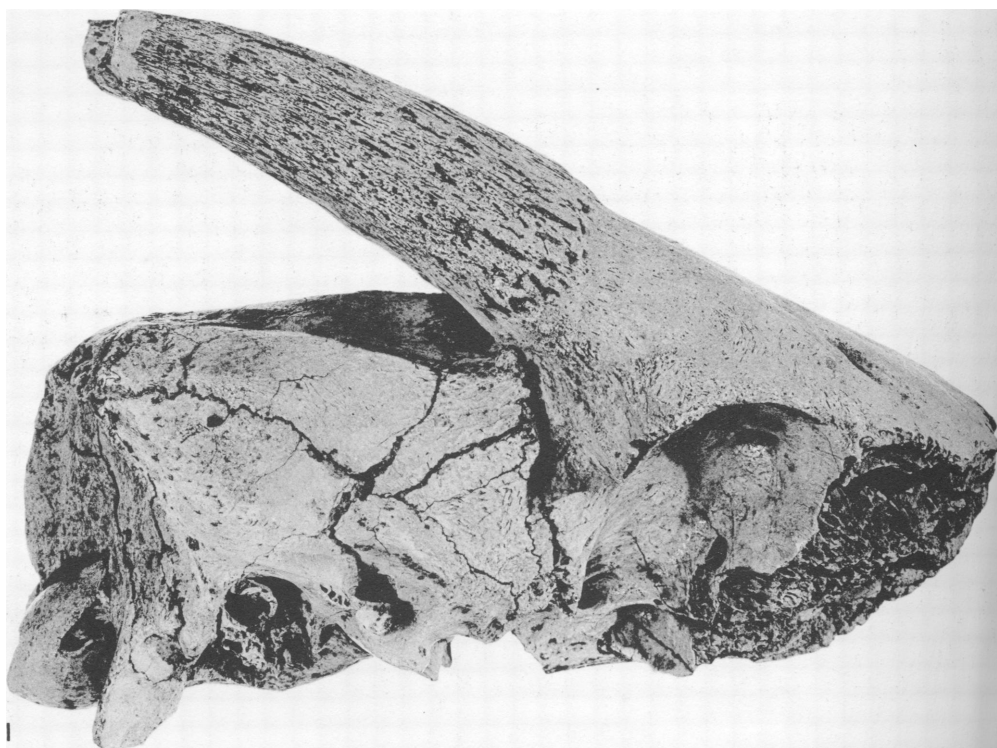
Bibos gaurus grangeri, new subspecies. Type, A.M.N.H. No. 18465, skull, dorsal view. One-fifth natural size



1-3, 5. *Bibos gaurus grangeri*, new subspecies. 1, 2. Type, A.M.N.H. No. 39211. 1. Upper dentition, right side, crown view. 2. Lower dentition, left side, crown view. 3. A.M.N.H. No. 39211, left metacarpal, dorsal view. 5. A.M.N.H. No. 39211, left metatarsal, dorsal view. 4, 6. *Bubalus bubalis* Linnaeus. A.M.N.H. No. 18485. 4. Left metacarpal, dorsal view. 6. Left metatarsal, dorsal view. 1, 2. One-half natural size; 3-6, one-third natural size



Bibos gaurus grangeri, new subspecies. Type, A.M.N.H. No. 18465, skeleton, right lateral view, not to scale

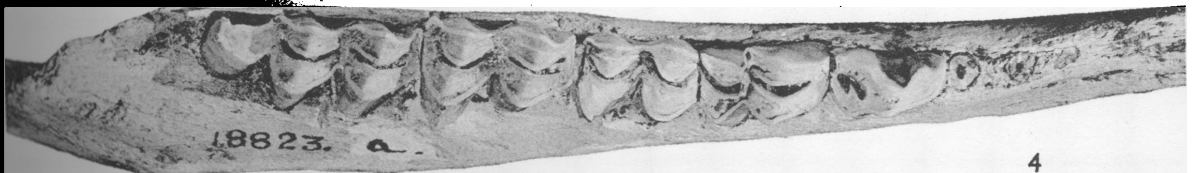
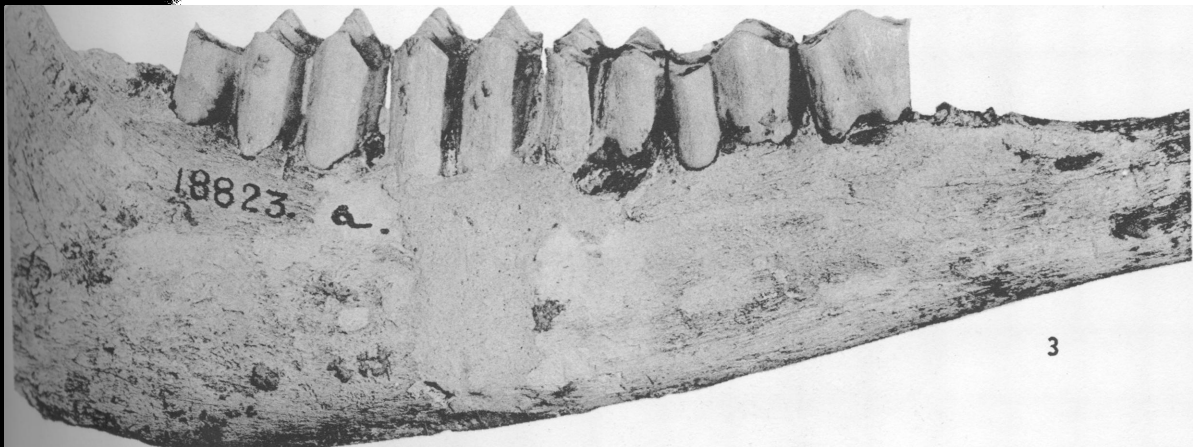
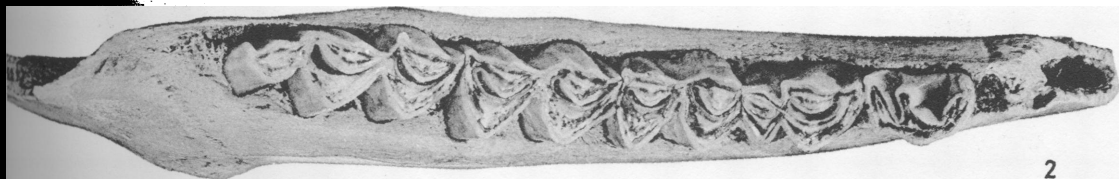
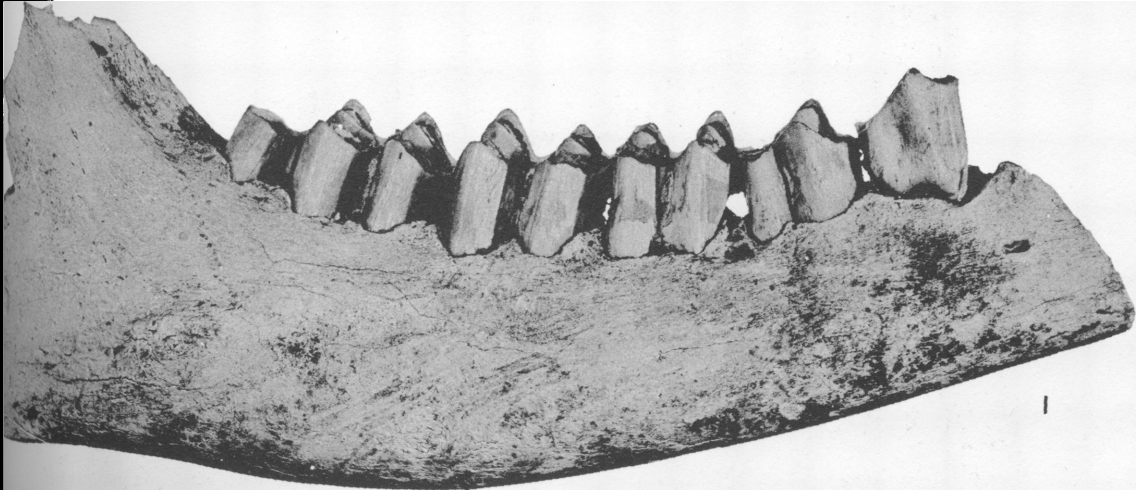


2

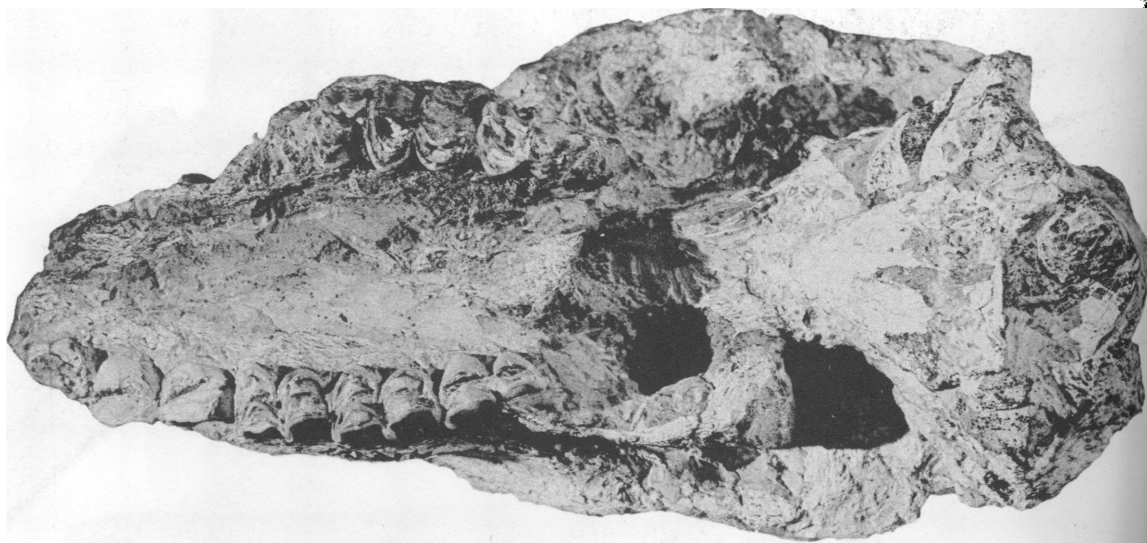
1. *Capricornis sumatraensis kanjereus*, new subspecies. Type, A.M.N.H. No. 18820, skull, right lateral view

2. *Naemorhedus goral* Hardwicke. A.M.N.H. No. 21787, crushed skull

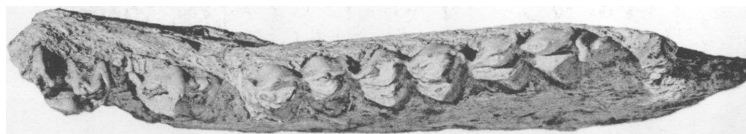
Both figures three-quarters natural size



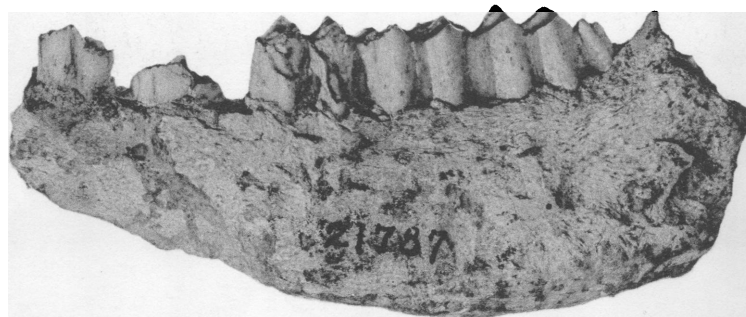
new subspecies. 1, 2. A.M.N.H. No. 18821, right mandibular ramus with
view. 3, 4. A.M.N.H. No. 18823a, right mandibular ramus with P₃-M₃.
All figures natural size



1



2



3

Naemorhedus goral Hardwicke. A.M.N.H. No. 21787, crushed skull and partial lower jaw. 1. Palatal view. 2, 3. Left mandibular ramus with P_2 - M_3 . 2. Crown view. 3. Lateral view. natural size